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OF ISRAEL

VOLUME I

FEBRUARY 1952

NUMBER 4

JERUSALEM



# BULLETIN OF THE RESEARCH COUNCIL OF ISRAEL

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3. Taylor, G.I., 1932, Proc. R. Soc. (London) A, 138, 41.

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



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# MORPHOLOGICAL SKETCH MAP OF SAFAD REGION



fig.1

- |   |                                |   |   |
|---|--------------------------------|---|---|
|  1 | BASALT PLATEAU OF DALLATA      |  2 | PLATEAU OF WADI TAWAHIN                   |
|  3 | MOUNT KANON, NORTH-WEST SLOPES |  4 | MOUNT KANON, SUMMIT AND SOUTH-EAST SLOPES |

DRAWINGS: DOV BLUMENFELD

# THE GEO-HYDROLOGY OF THE SAFAD REGION\*

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## A. AREA AND MORPHOLOGY

The area surveyed consists of the surroundings of the town of Safad in Upper Galilee and extends from the Safsufa-Meirion-Beth Shamai road at the foot of Mt. Azmon in the West to the Rosh-Pinna-Mahanayim road in the Hula-Jordan Valley.

The area can be subdivided into 4 major morphological units: (see morphological sketch, fig. 1)

1. The basalt-plateau of Dallata-Teitaba.
2. The plateau between Mt. Azmon and Mt. Kanan, which after the Wadi Tawahin passing through it, will be referred to as the plateau of Wadi Tawahin.
3. The north-eastern, northern and western slopes of Mt. Kanan.
4. The peak of Mt. Kanan and its eastern, south-eastern and southern slopes.

### 1. *The Basalt-Plateau of Dallata-Teitaba*

The northern section of our region includes parts of a high plateau 8 km<sup>2</sup> in area having basalt in its sub-soil. Its altitude is remarkably uniform and varies between 800 and 825 m above sea level. Only a few conical hills, remnants of old volcanoes, rise above this height (e.g. Dallata). An interesting morphological feature of the plateau is the scarceness of erosion valleys (Wadis).

The plateau terrain, facilitating agricultural cultivation, and the basaltic rock in the sub-soil, weathering into fertile soils, resulted in the concentration of Arab villages in this region. The lack of an adequate water supply, however, conditioned by the entire absence of springs resulted in the location of the Arab villages (Safsufa, Qadita, Teitaba, Ras-el-Ahmar) outside the plateau area or on its periphery (Teitaba). Dallata is the one exception, being located on the plateau.

The black to black-red soils and the rocky surface of the outcrops of hard black basalt determine the morphological characteristics of the Dallata plateau. The dark colours—the black of the basalt and the dark shades of the soils—predominate in the landscape.

\* This paper is part of the Ph. D. thesis of the author, under the tutorship of Prof. Y. L. Picard, of the Hebrew University, and is published here by permission of the Hebrew University authorities.



## 2. *The Wadi Tawahin Plateau*

The western boundary of the surveyed area is the eastern slope of the Mt. Azmon block. To the East of it, as far as the western slopes of Mt. Kanan extends a very rough and rocky terrain, the karstic plateau of Wadi Tawahin. Narrow and sometimes cañyon-like wadis have cut their courses deep into the landscape and dissect this region into a number of flat-topped hills. Thus the flat summits of these hills give the region the characteristics of a plateau. The elevation is quite uniform. It reaches in the North, near Safsufa and Meiron, up to 700 m and decreases slightly towards the South to about 650 m, east of Beth-Shamai. The hard dolomites and limestones, mostly of Cenomanian age (see morphological sketch, fig. 1) occurring everywhere on the surface as large and small blocks separated by narrow fissures, form a very ragged and rough karstic terrain. Even sinkholes and small dolines can be found there. The soils formed during the weathering of these rocks are of the red-brown terra-rossa type.

The karst morphology of the Wadi Tawahin plateau, renders its intensive agricultural use very difficult. Sufficient soil facilitating the growing of small orchards, vineyards and grains, has accumulated only in the narrow wadi courses and on the plateau itself in some small depressions. The Arab inhabitants used most of the lands for grazing. A successful attempt at afforestation in this region was made by the Jewish National Fund, near Khirbeth Qeiyumi on the Acre-Safad road. Somewhat better conditions prevail in the surroundings of Ein-Zeitim where softer rocks of Turonian age form a less rough terrain. Part of the Ein-Zeitim lands are situated here and are today cultivated, after removal of stones. Similar rocks also appear in the neighbourhood of Safsufa where soils can be improved in the same way\*. A foreign element in this morphological unit is the trough-like depression of triangular shape near Khirbeth Qeiyumi on the Acre-Safad road (see geological map Pl. I). There, the sub-soil is composed of chalk and marl of Senonian age (p. 8 No. 3). The weathering of these rocks, together with alluvial material washed down into the depression, has formed grey soils, easily cultivated and a smooth-surfaced terrain (see geological map, Pl. I white colour). These grey soils, however, are less fertile than the terra-rossa soils of the Wadi Tawahin plateau. The same rough terrain characteristic of the Wadi Tawahin plateau is also seen along the course of the Wadi Khallat-es-Siddiq, east of Teitaba. There too, it is conditioned by the Cenomanian and Turonian dolomites and limestones outcropping in the neighbourhood.

## 3. *Mt. Kanan*

Mt. Kanan comprises the eastern part of the area under consideration. It rises abruptly from its northern limit,—the Wadi Khallat-es-Siddiq—to its highest point near Biriya (Jebel Biriya 954 m), and from there descends gently towards

\* This is carried out at present by the Jewish National Fund.



the South. Mt. Kanan, from a morphological point of view, can be divided into two components: (a) The landscape of the northern, north-western, and western slopes is conditioned by the soft chalk and marl rocks of Senonian to Paleocene age which form a soft, smooth-surfaced landscape of rounded hills. The bright colours of the rocks, together with the light-grey colours of the soils originating from them, stand out in sharp contrast against the dark coloured basalt and basalt-soils of the Dallata plateau in the North as well as against the dark grey of the dolomitic rocks and the brown-red of the terra-rossa soils of the Wadi Tawahin plateau. Both soil and sub-soil in these chalky parts of Mt. Kanan (Senonian-Paleocene) are affected by very active erosion. Numerous parallel gullies and Wadis dissect the western slopes between Biriya and Ein-Zeitim, sometimes even forming bad-land morphology. (b) From the summit of Mt. Kanan near Biriya southwards and south-eastwards, there is a complete change in the appearance of the landscape. Here, hard limestones of Eocene age occur. Consequently the surface is again rocky, and the colour of the soils is again the brown-red of the terra-rossa. Karstic phenomena are, however, not as strikingly developed as in the Wadi Tawahin plateau, and the landscape has not the same rough appearance as there. Only in the most eastern and south-eastern parts of Mt. Kanan, near Rosh-Pinna and Amiad (Jub-Jussuf) the morphology is highly karstic, just as on the Wadi Tawahin plateau. The reason lies in the appearance here of hard crystalline limestones of Middle Eocene age.

In the East along the Tiberias-Metulla highway the area is bounded by the basalt-covered plains of the Jordan valley, which were not included in the present survey. These again form a kind of plateau—the basaltic plateau of the Upper Jordan valley.

Basaltic rocks, besides those of the Dallata plateau and those of the Jordan valley just mentioned, are found in several other localities in the area, such as Jebel Aswad ("The Black Mountain") and near the village of Mughr-el-Kheit. These occurrences are easily recognized in the landscape by the black colour of the rocks, but they are of little morphological importance since their area is somewhat restricted.

## B. FORMATIONS

The description of the formations is confined to the most general characteristic properties, without giving lists of fossils or entering into discussion of stratigraphic details.

### 1. *Cenomanian*

The Cenomanian is the oldest formation outcropping in the area surveyed. Most of the rocks of Mt. Azmon, the greater part of the Wadi Tawahin plateau and of part of Wadi Khallat-es-Siddiq belong to this formation. In the Wadi Tawahin plateau, the rocks are mostly hard dolomites and dolomitic limestones,

but there are also some limestones. Most of these rocks belong to the Upper Cenomanian. Their characteristic karstic weathering has already been mentioned. The complete thickness of the Cenomanian has not been determined since its base is not exposed; it certainly amounts to more than 300 m.

## 2. *Turonian*

Outcrops of this formation are also to be found on the Wadi Tawahin plateau, especially in its eastern parts, and along the course of Wadi Khallat-es-Siddiq. The rocks of the Turonian are mainly crystalline limestones occurring in reefs, and smooth lithographic limestones of the type known in the Jerusalem area as "Mizzi Hellu". Dolomitic limestones also occur. The thickness of the Turonian in this area is 60–70 m. The Turonian landscape generally displays features similar to the Cenomanian, but is sometimes less rocky and ragged. The soils formed by weathering of the Cenomanian and Turonian rocks are characterized by their red colours ("terra-rossa").

## 3. *Senonian*

The Santonian, following on top of the Turonian, can be subdivided into Santonian, Campanian and Maestrichtian. The occurrence of Danian has not been established so far.

The Santonian, (see Plates I and II), the lowermost part of the Senonian, occupies extensive areas on the northern slopes of Mt. Kanan, north of Ein-Zeitim and on its western slopes below Safad, and Dhahiriya-et-Tahta. The characteristic rocks of the Santonian are hard chalky limestones, containing reddish stripes, especially in their lower layers. These rocks resemble the "Kaakule" of the Santonian in the Jerusalem area. They are much softer than the rocks of the Turonian–Cenomanian, and therefore do not display the same karstic features and rough landscape. The soils forming on the Santonian, however, are still red-coloured—possibly because of the silica content of these hard chalks. Thus the Santonian constitutes petrologically and morphologically the transition from the hard, dark-grey coloured rocks of the Cenomanian–Turonian to the soft, glaring white chalks of the Upper Senonian–Paleocene. The hard chalk of the Santonian was always a favourite building and ornamental stone of the inhabitants of this area, as shown by its use in their houses as well as the many quarries, both old and new.

The Campanian (see Plates I and II) also outcrops on the northern and western slopes of Mt. Kanan. The best exposures are situated near the settlement of Ein-Zeitim on the Acre–Safad Road. The lower layers of the Campanian are formed by marls and shales whereas the upper portion consists of chalky limestones. All the rocks of the Campanian are more or less bituminous. They display a glaring white colour on their outer surface whereas they are dark-grey to black coloured on fresh surfaces, because of their bitumen content. The almost impervious marls give rise



to a water horizon (see Hydrology, p. 14). The thickness of the Campanian is about 60—70 m. The soft chalk and marls, together with similar soft rocks of the formations following above the Campanian, give the landscape the characteristic bright colour of the Palestinian Senonian-Paleocene. The bituminous chalks could possibly be used for various industrial purposes.\*

The Maestrichtian (see Plates I and II) consists mostly of white chalks and chalky limestones, but includes also some thin layers of black flint bands and flint lenses as well as phosphatic limestone. The rocks sometimes contain small lumps of asphalt. This formation appears mainly in the higher parts of the northern and western slopes of Mt. Kanan. Good exposures are located above the Wadi-el-Amiq near Biriya and on the Acre—Safad road, about 200 m SE of Ein-ez-Zeitun. The thickness of the Maestrichtian is about 40 m.

The total thickness of the Senonian amounts therefore, to about 150 m.

#### 4. *Paleocene*

The Paleocene covers vast areas on Mt. Kanan reaching from Qaba'a NW of Firim on its north-western slopes over Biriya and Safad to Aqbara in the South. It consists of a 100m thick series of alternating chalk, shales and marl. The question, if the lower part of this series represents Danian, is still unsettled, and is being studied now by micro-paleontological methods. The rocks partly are somewhat bituminous and contain limonite, which appears both as larger concretions and in stripes and specks and as thin films associated with joints. The Paleocene, in its petrological character resembles the underlying Senonian, more than the Eocene following on top. The marls give rise to a water horizon in the upper layers of the Paleocene (see Hydrology, p. 14.).

#### 5. *Eocene*

The Eocene rocks out-cropping on Mt. Kanan belong to the Lower and to the Lower-Middle Eocene.

##### a. *Lower Eocene*

Just below the settlement of Biriya, near the entrance to the town of Safad, and at numerous other localities in the area, a more resistant stratum appears above the soft Paleocene rocks, sometimes forming cliffs easily recognized in the landscape. With this layer starts an 80 m thick series of well-bedded limestones, still chalky in the beginning, but becoming harder as one proceeds upwards. This series contains many brown flint concretions. On account of the position of this series above the Paleocene and below the Middle Eocene, it is tentatively attributed to the Lower Eocene.

\* The investigation of the bituminous rocks from this region is being incorporated in a general survey of bituminous material, which forms one of the projects of the Research Council of Israel.

Because of the harder character of the rocks of this well bedded series, the landscape again displays a rougher surface (contrasting with the landscape of the underlying Senonian-Paleocene) and also gives rise to red-brown soils. Like the Santonian, forming the transition from the hard rocks of the Cenomanian-Turonian to the soft Senonian-Paleocene, the lower Eocene is the transition from these formations to the hard limestones and crystalline limestones of the Middle Eocene.

### b. *Middle Eocene*

On the eastern slopes of Mt. Kanan, and on its south-eastern parts near Rosh-Pinna and Amiad (Jub-Jussuf) the Lower-Eocene bedded flinty-chalky limestones and limestones are overlain by hard, smooth, lithographic limestones again resembling the "Mizzi Hellu" of the Jerusalem area (see Pl. I and II). The thickness of this limestone series amounts to about 40 m. On top of it follow crystalline limestones. Their total thickness could not be established, because no layers topping them conformably are found in our area. The maximum thickness of the crystalline limestones observed is also about 40 m. The limestones and crystalline limestones of the Middle Eocene again form an extremely karstic landscape.

The total thickness of the Eocene in the area is therefore about 160 m.

The thicknesses of the various sedimentary formations building up the Safad region can thus be summarized, as follows:

Eocene (Lower-Middle)	160 m
Paleocene	100 "
Senonian	150 "
Cenomanian-Turonian	400 " (minimum)

### 6. *Basalt*

As already stated, basaltic rocks occur in the area in the North, in the Dallata-Teitaba region, and near Qaba'a and Mughr-el-Kheit. The basalt of Jebel Aswad, near Qaba'a and that below the village of Mughr-el-Kheit are worth mentioning. On account of the sharp western boundary of the basaltic cover, which coincides in both cases with fault-lines, one can assume that at these localities eruption took place in the fault zone, and that the lavas streamed from there eastwards in the direction of the Jordan valley. The basalt in our area generally is very hard, and sometimes gives rise to a "sea of rocks". Its appearance in connection with young fault-lines and comparison with basalts from Lower Galilee indicate a Plio-Pleistocene age. This assumption, however, has yet to be proved by more exact petrological studies.

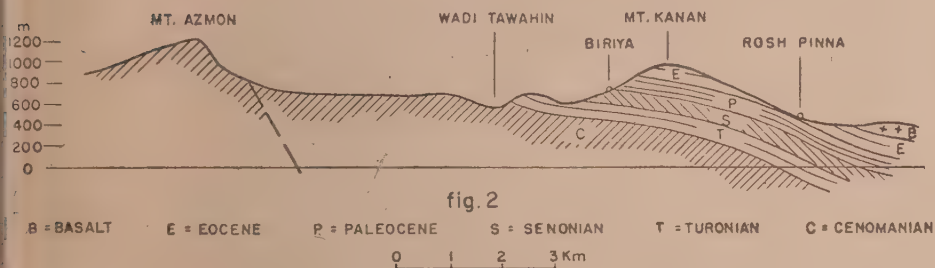
### C. *TECTONICS*

As demonstrated by the general geological section (fig. 2) the area constitutes an anticlinal upwarp. From this upwarp, however, only part of the crest (the Wadi



Tawahin plateau) and the eastern limb (Mt. Kanan) are preserved, whereas another part of the crest and the western limb are represented by the elevated block of Mt. Azmon, forming a separate tectonic unit. Consequently, the strata are horizontal in almost all parts of the Wadi Tawahin plateau, but on Mt. Kanan, there appear dips to the East and South-East, increasing in steepness towards the Jordan valley in the East.

### SCHEMATIC GEOLOGICAL CROSS-SECTION from MT. AZMON to ROSH PINNA



From morphological and general geological evidence one must assume that a major fault zone separates Mt. Azmon from the Wadi Tawahin plateau. Such a fault zone presumably passes along the Acre—Safad road, between Beth-Shamai (Es-Samnuj) and Meiron lying on the boundary of the surveyed area. It has not been included in the present survey and is not represented on the map.

Another major fault zone might be presumed at the eastern foot of Mt. Kanan, along the line Firim—Rosh-Pinna, but our survey has shown that no such fault exists there. Instead the strata of Mt. Kanan bend down in a sharp, eastwards directed flexure, straighten out again and dip down gently below the basaltic flows and the other young formations (Pliocene-Pleistocene) of the Jordan valley. This result is proved by the outcrops of Eocene rocks near the customs station at Rosh-Pinna and to the North of it, as well as by the wells of Rosh-Pinna and Mahanayim, where Eocene limestone was encountered in depths of 100—200 m. We have, therefore, to assume, that the big Graben fault of the Jordan valley—if this exists at all in our area—is situated farther east and covered by the young formations of the Jordan valley.

The other smaller faults of the area can be subdivided into two groups:

1. Faults more or less diagonal to the Jordan valley direction occurring mainly in the eastern section of the area.
2. Graben-like structures in the neighbourhood of the Dallata plateau and north of Mt. Kanan.

1. *Diagonal faults*a. *The faults of Dhahiriya-el-Fauqa*

South of the Safad—Rosh-Pinna road near the small woods along the road, a conspicuous plain stands out in the landscape. Here, two faults, (1.a.1 and 1.a.2) running in a NW—SE direction, form a Graben-like structure and resemble therefore the structures described under (2). Their direction, however, affiliates them to the group of the diagonal faults.—The southern fault (1.a.1) runs from Deir-el-Hamra, passing through the sharp bend of Wadi Baqr (which might be caused by it) in a south-easterly direction, and possibly continues as far as Amiad. Its throw of 80—100 m brings crystalline limestone against well-bedded and hard limestone both of Eocene age.—The northern fault (1.a.2) passes from el-Gharbiya in the direction of the pine woods on the Safad—Rosh-Pinna road. It throws crystalline limestone against hard limestone and the uppermost layers of the well-bedded limestone, with a throw of 70—80 m.

b. *Mt. Kanan fault*

This fault runs from a point 500 m north of the tomb of Sheikh Muhammad Hadid on the summit of Mt. Kanan in a SSE direction as far as the oliveyard near the bends of the Safad—Rosh-Pinna road. Its continuation in the direction of the Wadi-el-Eish is not certain. Its throw amounts to 40—60 m, and brings crystalline limestone against hard limestone (both of Middle Eocene age).

c. *El-Mughra fault*

This fault runs from el-Manazil through el-Mughra towards the Wadi Abu Musawar. But it can not be followed as far as the Wadi. Its throw is about 40 m.

d. *Jebel Aswad—Firim fault*

This fault starts at the western shoulder of Jebel Aswad and passes in a SE-direction towards the market hill of the village of Firim (300 m east of the village). It is cut by two diagonal faults (see e. and f. below) reaching it from the North, the one coming from Ammuqa, the other from Mughr-el-Kheit. It is not clear whether this fault continues into the Jordan depression, covered by alluvium, basalt and other young formations. Putting Senonian and Paleocene on its SW-side against Lower Eocene (well bedded limestone and chalky limestone with flint) on its NE-side, it is the most important fault on Mt. Kanan. The throw of about 150 m decreases towards the SE—similar to that of the el-Mughra and Mughr-el-Kheit faults (c. and e.).



e. *Mughr-el-Kheit fault*

This small fault runs from just below the village of Mughr-el-Kheit towards the Jebel Aswad fault in a NS direction. The throw is about 40 m.

f. *Ammuqa fault*

This is a fault of considerable throw (200 m). It places Turonian and Santonian against Paleocene and Lower Eocene. The basalt of Jebel Aswad appears at the junction of this fault with the Jebel Aswad fault. The basalt apparently ascended along the fault zone and flowed downwards almost as far as Mughr-el-Kheit.

2. *Faults on the Wadi Tawahin plateau and between the Dallata plateau and northern Mt. Kanan*

a. *The Graben of Jebel Shamakh*

On Jebel-Shamakh, south of Dallata, exists a WNW-ESE oriented Graben structure composed of three faults. The fault on the southern border of this Graben may be the continuation of the Jebel Aswad-Firim fault. (1.d). Its throw is about 20 m. The northern fault shows a greater throw of 40 m. The throw of the central one is about 20 m. In the depression between the central and the northern fault Maestrichtian and Campanian appears in contact with harder Santonian rocks on the upthrow side. The structure and the different hardness of the rocks have formed a natural trench, which is a strange and conspicuous feature in the landscape.

b. *Ein-Zeitim Block*

Two faults, Jebel Hashusa fault (2.b.1) and Ein-Zeitim fault (2.b.2), directed NE-SW cause the block-like structure of Jebel Hashusa and Jebel Bir-esh-Sheikh.

The Jebel Hashusa fault (2.b.1) passes from a point south of Teitaba in the direction of Wadi Amiq without, however, reaching it. It places Santonian on its SW side against Campanian and Santonian on its east side. The throw is about 60 m. The Ein-Zeitim fault (2.b.2) runs from Bir-esh-Sheikh along the Acre-Safad road as far as the old settlement of Ein-Zeitim. It places Turonian on the SW upthrow side against Santonian on the NE downthrow side. The throw is about 50 m.

c. *The Khirbet-el-Qeiyumi Graben*

A fault runs from Bir-esh-Sheikh towards Manazil-el-Lauza (2.c.1) placing Turonian and uppermost Cenomanian against Campanian and Santonian. It is possibly the continuation of the Ein-Zeitim fault. Its throw is 50-70 m. This fault together with another fault (2.c.2) starting south of Teitaba and passing near Khirbeth Qeiyumi towards Manazil-el-Lauza forms a triangular-shaped dropped block. This fault

again places Turonian and Cenomanian against Campanian and Santonian and its throw is a little greater than that of the southern fault.

The Ein-Zeitim Graben (2.b) and the Kh. Qeiyumi Graben (2.c) form a tectonically as well as morphologically depressed area. (The dip of the strata in the Jebel Biresh-Sheikh does not show the general SE direction but tends to the West, towards the Kh. Qeiyumi Graben).

Summarizing the tectonics of our area we reach the following conclusions:— The Safad region constitutes an upwarp cut off near Mt. Azmon by a major fault zone. Mt. Azmon is therefore, a separate block representing the western raised limb of this large anticline. The Wadi Tawahin plateau with its horizontal strata, comprises the centre of the anticline and Mt. Kanan its eastern limb, dipping down into the Jordan Depression, where younger formations overly it unconformably. On the northern and eastern slopes of Mt. Kanan, a number of diagonal faults occurs, but only one of these is of major importance (Aswad—Firim Fault, 1.d). A special tectonic feature is the depressed area of Ein-Zeitim—Khirbet-Qeiyumi, situated near the centre of the upwarp.

One may safely assume that the folding occurred, as in other parts of Palestine at the beginning of the Miocene. The greater part of the faults, however, is of younger age (Plio-Pleistocene) as indicated by their appearance in the morphology. Well preserved fault plane surfaces and slickensides phenomena sometimes suggest a very young age of the faults. The high seismic activity in the Safad region is another indication of recent tectonic processes.

## D. HYDROLOGY

### 1. *Rainfall*

Annual rainfall quantities in the western parts of the area (Wadi Tawahin and Dallata plateau) are 1,000 mm, and even 1,100 mm on Mt. Azmon, beyond its Western boundaries. From the summit of Mt. Kanan eastwards, rainfall rapidly decreases to 800 mm at Rosh-Pinna and 400–600 mm in the Jordan Depression east of Rosh-Pinna. As compared with other areas in Palestine, these amounts of rainfall are very large.

### 2. *Surface Drainage*

The main drainage arteries in our area are the Wadi Tawahin, called Wadi Leimun and Wadi Amud in its lower tracts, and the Wadi Khallat-es-Siddiq. The Wadi Tawahin originating near Teitaba flows into the Lake of Galilee. All the Wadis draining the eastern and south-eastern part of Mt. Azmon (Wadi Meiron, Wadi Abu Yabis, Wadi-el-Jug, etc.), as well as those which effect the drainage of the north-western and western parts of Mt. Kanan (Wadi-el-Hamr, Wadi Jaj, Wadi Kharrar, etc.) feed the Wadi Tawahin. The Wadi Khallat-es-Siddiq drains the northern and north-eastern slopes of Mt. Kanan and the eastern parts of the Dal-



lata plateau, flowing in an eastern direction (Wadi Jebel Shamakh, Wadi Abu Imara, Wadi Nabratein, Wadi-el-Bustan). This Wadi flows into the Hula south of Yessod-Hamaala. The drainage of the eastern slopes of Mt. Kanan from Qaba'a to Rosh-Pinna is effected by Wadis flowing towards north-east and abutting finally into the Jordan, south of Lake Hula. The eastern slopes of Mt. Kanan south of Rosh-Pinna are drained by the Wadi Abu Mussawar, abutting directly into the Lake of Galilee, near Kefar Nahum.

The main watershed in our region divides the drainage-area of the Wadi Tawahin conducting its waters southward into the Lake of Galilee, from the drainage area of the Wadi Khallat-es-Siddiq and the other Wadis leading eastward or northwards into Lake Hula or into the Jordan river. It runs from Teitaba first in a SE-direction towards Biriya, and there turns in a SSE-direction.

The drainage of the area south of Rosh-Pinna is directed southwards into the Lake of Galilee, by way of Wadi Abu Mussawar.

### 3. Springs

#### a. *Springs connected with perched water horizons (see hydrological sketch, fig. 3)*

In our area two perched water tables exist giving rise to two corresponding horizons of springs. The upper horizon is situated within the chalk-marl series of the Paleocene. The springs belonging to this horizon are found along a crescent-shaped line on the heights of the northern and western slopes of Mt. Kanan. The springs of Firim, the el-Bustan springs, the springs near Biriya, near the Arabic village of Biriya, and those near the road leading into Safad belong to this group. Other springs originating in the same Paleocene strata are situated near Qaba'a, as well as in the Wadi Jauna, above Rosh-Pinna, where a Paleocene "window", appears in the bed of the Wadi, below the Eocene, building up the entire south-eastern slopes of Mt. Kanan.

The yield of the springs of this group situated between Qaba'a and Safad is rather small, and they partly or entirely dry up in the course of the rainless summer months. The reasons are the restricted intake area of the springs (being located at considerable heights), the poor cover of the impervious beds, their origin against the dip of the strata and their relatively anticlinal position.

South of Safad, as well as in the Wadi Jauna above Rosh-Pinna, and in Wadi Firim, the springs have a more extensive intake area, more extensive cover and, on the eastern slopes of Mt. Kanan, the eastward dip is an additional favourable factor. Thus the yield of the three Rosh-Pinna springs is about  $20 \text{ m}^3/\text{hr}$  during the summer months, and that of the Firim springs about the same. Ein Hamra et-Tahta, south of Safad yields  $5\text{--}10 \text{ m}^3/\text{hr}$  in summer, Ein Hamra el Fauqa  $3\text{--}5 \text{ m}^3/\text{hr}$ .

Another perched water table exists at the boundary between the Campanian marls and chalks. To this horizon, too there corresponds a group of springs en-

## HYDROLOGICAL SKETCH MAP OF SAFAD REGION

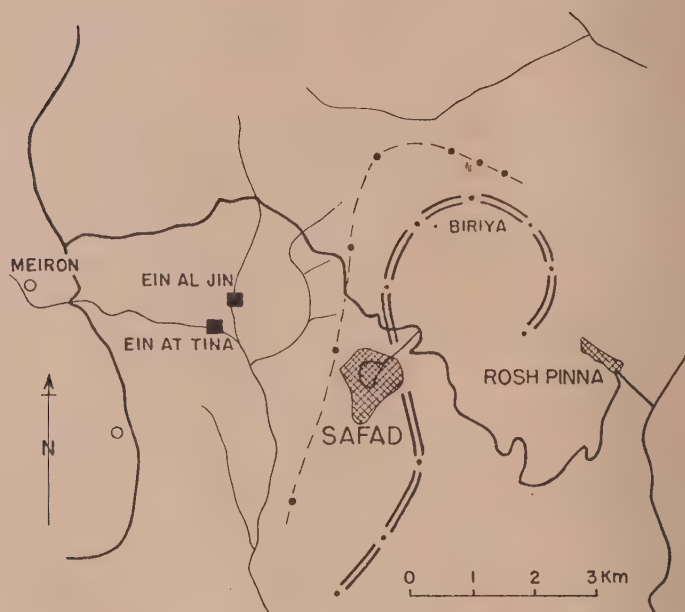


fig.3

- SPRINGS ON FAULTS (?)    ■ KARSTIC SPRINGS  
 - - - - - SPRINGS OF CAMPAIAN HORIZON    —•— SPRINGS OF PALEOCENE HORIZON

circling the northern and western slopes of Mt. Kanan in a crescent-shaped line. Because of lack of outcrops of Campanian on the north-eastern part of Mt. Kanan, this line of springs begins only with the Wadi Nabratein, passing on from there through Ein-Zeitim, Ein-ez-Zeitun, Dhahiriya-et-Tahta as far as Ein Wuhush, SE of Safad. The yield of this Campanian group of springs on the western slopes of Mt. Kanan is somewhat larger than that of the Paleocene springs in the same region, because of the lower elevation of this water horizon, the better cover and the more extensive intake area. The proximity of the crest of the anticline, however, makes itself felt here too, and none of the springs yields more than  $5 \text{ m}^3/\text{hr}$  and many of them yield considerably less water. The Ein-Zeitim springs, situated in the Wadi Ein-el-Barraniya, yield only about  $3 \text{ m}^3/\text{d}$  during the summer months.\*

\* The Safsufa and Goosh-Halay springs beyond the boundaries of the surveyed area also belong to this Campanian water horizon.



### b. *Springs connected with fault zones*

No springs caused entirely by faults exist within our area. It is, however, possible that faults have some influence on the occurrence of the springs near Ammuqa, but still, as evident from their stratigraphic position and their small yield, they are in the first place springs of the Paleocene water horizon. The springs of Meiron, Beth-Shamai (Es-Sammuj) at the foot of Mt. Azmon as well as those of Farradiya on the south-eastern foot of Mt. Azmon, all outside our area, show possibly the stronger influence of fault conditions on their origin.

### c. *Karst-springs*

Important springs of considerable yield originate in the Wadi Tawahin (Ein-el-Jin) and in the Wadi Meiron near its confluence with the Wadi Tawahin (Ein-et-Tina). There is no evidence of impervious strata or of faults which might be the reason for the appearance of springs here. On the other hand, the highly karstic nature of the Wadi Tawahin plateau suggests that these be defined as karstic springs. Their yield is large compared with that of the other springs in the area. Ein-et-Tina yields 50–75 m<sup>3</sup>/hr during the summer: the yield of Ein-el-Jin (Devil's spring) varies periodically – the period being several hours to less than one hour – between 20 and 45 m<sup>3</sup>/hr. This phenomenon of periodicity strengthens the impression that these springs are of a karstic character. The town of Safad receives its present water supply from Ein-et-Tina in Wadi Meiron.

Thus we find fault-conditioned springs only outside our surveyed area at the foot of Mt. Azmon, karstic springs in the region of the karstic Wadi Tawahin plateau, and springs connected with impervious strata on Mt. Kanan, with its rather impervious chalks and marls. The basaltic Dallata-Teitaba plateau is noticeable for its entire lack of springs.

## 4. *Hydrological conclusions*

From the results so far achieved regarding the geological structure, springs and rainfall in our area we can arrive at the following conclusions about underground-water conditions.

### a. *Direction of underground drainage*

The main direction of underground drainage in the eastern part of Mt. Azmon is – as shown by the springs from Farradiya to Meiron – towards the East. (It is possible that the springs on the Wadi Tawahin plateau receive part of their water from Mt. Azmon). From the structure of Mt. Kanan we conclude that the underground drainage there is directed towards the south-east. The drainage base for our area, therefore, is not the Mediterranean sea, but the Lake of Galilee. The underground drainage of the northeasternmost parts of Mt. Kanan, north of the Jebel Aswad-Firim fault, is possibly directed towards Lake Hula.

### b. *The underground water-level*

The depth of the main underground water-level for the eastern rim of our area can be fixed by the elevation of the springs of the Hula Basin in the North and the elevation of the Lake of Galilee in the South. Thus we find an elevation of 70 m (above M.S.L.) for the underground water level in the Rosh-Pinna region.

There is no possibility so far to reach any definite conclusions as to the elevation of the main underground water-level within the mountainous area. Drilled wells do not exist here. One might ask if the springs of the Wadi Tawahin plateau, originating at an elevation of +525 m, represent the overflow of the main underground water table. But under such an assumption we would have a very steep rise of the water level from the Lake of Galilee to Safad (50 m for every km). It remains for future drillings in the mountainous areas of the country to clear up this question, which is of major importance for the development of underground water resources in the high mountains of Galilee.

### SUMMARY

The geological conditions of the Safad region have been mentioned by the earlier geologists who visited the country. e.g. Lartet and Conrad. Blanckenhorn was the first to present a concise picture of the stratigraphy. But the two principal sources of information on the geology of upper Galilee are L. Picard's "Structure and Evolution of Palestine" and the Provisional Geological Map of Safad on a scale 1:100,000 by G. S. Blake.

Picard's book contains a thorough study of the structural elements of which upper Galilee is composed. According to him, two major upwarps exist in central-eastern Galilee; the one is the central Galilean upwarp with its downfaulted crest near Mughar, the other is the upwarp of the Manara-Hunin mountains, bordering the Upper Jordan valley in the West. This latter upwarp might well represent the western limb of the Hermon anticlinorium on the other side of the Jordan valley, separated from it by the young rift. It is interesting to compare the geological structure of the Hula Basin and Upper Jordan valley in the North near Manara-Hunin-Khalsa, with the mountain border in our region. In the North a definite border fault exists, and the strata dip away from the Jordan valley in a westward direction, leading into a large synclinal basin with Eocene rocks – most of it on Lebanese territory. But in the area of Mt. Kanan – Rosh-Pinna, more to the South, we find a strong flexure of the strata to the East, and no fault line could be detected. Parallel with this structural difference goes the greater topographic elevation of the Jordan valley south of Lake Hula, compared with the Northern Hula – Upper Jordan valley. This indicates that in our area a swell exists in the long Jordan valley, separating the Hula from the Lake Galilee Basin. Instead of a true Graben, we find a more synclinal structure. This also has been pointed out already by Picard.



The transition zone between the "anticlinal Graben" in the North and the "synclinal basin" in the Rosh-Pinna region is easily recognized on the mountain border in the Mughr-el-Kheit—Marus region, where a large number of transversal faults and evidence of young volcanic activity indicates a zone of special tectonic weakness.

Mt. Kanan, with its south- and south-east dipping strata, fits well into the general pattern of "tilted blocks" of eastern Galilee. One can follow these tilted blocks from Wadi Hindaj north of Rosh-Pinna as far as Hittin—Yavneel on the Lake of Galilee and even to the Nebi-Dahi (Givath Hamoreh) in the Emek Jesreel.

The attached geological map constitutes a revision of Blake's survey, the principle difference being in the interpretation of the Turonian formation and the more detailed stratigraphic division of the Senonian and Eocene formations.

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SOIL AND LEAF ANALYSES AS INDICATORS OF FERTILISER  
REQUIREMENT IN SHAMOUTI ORANGE GROVES \*

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## INTRODUCTION

The nutritional status of orange trees in Israel differs considerably in different groves and frequently even in the same orchard. The soil of the main orange region is characterized by the extreme variability of its properties which may change considerably even over small distances in the same grove. In addition, stocks and scions in most groves are genetically unhomogeneous and therefore possess varying capacities of nutrient absorption and translocation. The differences in fertiliser requirements of individual groves became even larger during the prolonged crisis of the citrus industry in this country (which began in 1937 and lasted for over 10 years) when growers were forced to abandon the customary methods of fertilisation. In most commercial groves cultivation and fertilisation were reduced to a minimum. Each grower fertilised his grove according to his means, and the quantities and kinds of fertiliser used differed widely.

Consequently it was deemed desirable to develop a method for estimating the fertiliser needs of individual orange groves. Two chemical methods have been widely used for this purpose: quick soil analyses and analyses of the leaves or of other suitable parts of the plant. Their use and theoretical foundation have been discussed in comprehensive reviews<sup>6,18</sup>.

Leaf analyses have been used successfully for citrus by Hardy<sup>21</sup>, Chapman<sup>12</sup>, Bathurst<sup>3</sup>, Haas<sup>23</sup>, Innes<sup>25</sup>, and in Israel by Oppenheimer<sup>30</sup> and Winnik<sup>17</sup>.

Soils tests in orange groves were made by Innes<sup>25</sup>, Hume<sup>24</sup>, Chapman<sup>11</sup> and Coit<sup>13</sup> under varying conditions which sometimes differed considerably from conditions here) with varying results. Whereas Hume<sup>24</sup> and Coit<sup>13</sup> do not advise the use of soil analyses in citrus groves, both Innes<sup>25</sup> and Chapman<sup>11,11</sup> found them adequate for testing certain nutritional requirements. Chapman advocates nitrate analyses in soils for estimating the nitrogen needs of groves. Innes, however, considers this soil test as inconclusive but recommends the analysis of soil phosphates as an indicator for the phosphorus requirements of trees.

\* Received September, 1950.

<sup>1</sup> This is an abridged translation of part of a Hebrew thesis presented for the Ph. D. degree at the Hebrew University, Jerusalem, in 1949.



In view of such opposed findings, experiments were undertaken in order to examine the relative value of soil and plant analyses in estimating the nutritional requirements of local orange groves. Suitable methods for both tests were also to be developed. As nitrogen and phosphorus comprise the main—and often the only—nutritional elements supplied to local groves by fertilisation, the present investigation was confined to nitrogen and phosphorus.

#### EXPERIMENTAL GROVES

All experimental groves were situated in the southern and central parts of the coastal plain of Israel—the main orange region of the country. In two of the groves, experiments in the rejuvenation of neglected orange groves and the influence of fertilisation upon it were carried out by Oppenheimer<sup>31</sup>. The groves and the lay-out of these experiments have been described in detail by him. All trees were Shamouti orange grafted on sweet lime stock, except those in Grove D where the stock was sour orange. Planting distances were  $4 \times 4$  or  $5 \times 5$  metres.

Grove A is situated at the slope of a hill near Rehovot. Here the smaller soil particles were washed from the top to the lower part of the hill, as was suggested by the mechanical analysis of the soil (Table I). Whereas the soil at the top of the hill contained only 6.5% of silt and clay in the upper 0-90 cms, 13.5% of these fractions were found at the lower part of the hill.

TABLE I

*Mechanical composition of the soil in Grove A. (% of soil dried at 105° C)*

Soil level (cm)	SLOPE OF THE HILL			TOP OF THE HILL		
	Coarse sand	Fine sand	Silt and clay	Coarse sand	Fine sand	Silt and clay
0—30	10.2	75.6	14.2	8.2	85.6	6.2
30—60	11.0	75.4	13.6	8.3	85.8	5.9
60—90	12.8	74.6	12.6	11.3	81.3	7.4

The soil was a typical "kurkar" sand rich in lime (Table II).

TABLE II

*Lime percentage and pH in the soil of Grove A*

Soil level (cm)	CaCO <sub>3</sub> (%)		pH	
	Slope	Top	Slope	Top
0—30	10.3	22.4	8.12	8.28
30—60	20.8	25.3	8.24	8.42
60—90	27.3	24.0	8.36	8.52

Experiments were carried out in 4 fertilisation plots, all of which were situated in the upper part of the grove. They received: 1) No fertiliser; 2) 2 kg of superphosphate per tree per year; 3) 1 kg of ammonium sulphate per tree per year; 4) 1 kg of ammonium sulphate and 2 kg of superphosphate per tree per year. Four central trees in each plot were sampled for leaf analyses, and around each of these trees soil samples were taken. In the other groves too, the same method of sampling was used.

Grove B is planted on a slightly loamy sand (Table III).

TABLE III

*Mechanical composition and pH of the soil in the northern part of Grove B  
(composite soil sample of 24 locations)  
(% of soil dried at 105° C)*

Soil level (cm)	Coarse sand	Fine sand	Silt and clay	pH
0—30	2.06	86.74	10.94	7.39
30—60	2.18	84.74	12.81	6.83
60—90	2.33	83.25	13.88	6.90

This grove, previously neglected, was reestablished during the rejuvenation and fertilising experiments from 1943 to 1947 and was afterwards completely neglected again. The nitrogenous fertiliser used was a cotton seed meal containing 4.5% N, 2.5%  $P_2O_5$ , 2.5%  $K_2O$ . Tests were carried out in the plots with each tree receiving the following fertilisation per year: 1) No fertiliser. 2) 5 kg of cotton seed meal, 3) 5 kg of cotton seed meal and 2 kg of superphosphate.

Grove C is situated on a soil similar to that of grove B (Table IV).

TABLE IV

*Mechanical composition and pH of the soil in Grove C (composite sample of  
24 locations; soil dried at 105°C)*

Soil level (cm)	Coarse sand	Fine sand	Silt and clay	pH
0—30	3.42	84.52	11.85	7.60
30—60	3.29	87.11	9.35	7.68
60—90	2.92	85.46	11.23	7.54

The grove was well cared for but not fertilised during 4 years (1940–43). In 1944 the uniform nitrogen fertilisation of the grove was renewed. Because of the extremely coarse fruit a phosphorus deficiency was suspected and superphosphate was applied in differential amounts by two methods. Treatments marked in the following as (a) consisted of superphosphate applied at a depth of 20 cms in holes made with a soil auger, while in (b) superphosphate was dissolved in water and applied with irrigation. The following fertiliser treatments were initiated in 1945:



1) control, 2) 1 kg of superphosphate (a), 3) 1 kg of superphosphate (b), 4) and 5) 2 kg of superphosphate (a) and (b), resp., per tree per year. The experiment in Grove C was of small dimensions as only 4 trees per treatment were used, each tree being considered a replicate.

Grove D is a commercial orchard planted on a loamy sand, is well cultivated, adequately fertilised and yields good returns. It was chosen as representative for a Shamouti grove in good condition.

## METHODS

### *Leaf composition*

Leaf samples were collected and prepared for analysis as recommended by Oppenheimer<sup>30</sup>, who slightly modified methods described earlier by Bathurst<sup>4</sup>. The percentage of the total nitrogen in dry matter of foliage was determined by the micro-Kjeldahl method of Parnas and Wagner<sup>33</sup>, and total phosphorus was determined by King's<sup>28</sup> method.

### *Soil composition*

Soil samples were taken with a cylindrical borer at 4-6 places around each tree used for leaf sampling, at a distance of 1 or 2 metres from the trunk. Sampling places were not scattered at random but chosen only within the irrigation basins. These basins constituted about 80% of the total area in the experimental groves. All fertilisers and manures were applied in the basins. Two soil samples from the same soil layer were combined for analysis.

Soil carbonates were determined by aid of a Scheibler calcimeter and soil nitrates by the phenol-disulphonic acid method<sup>2</sup>.

Considerable difficulties were encountered in finding a method for determination of available phosphorus in soil since most of the proposed quick methods do not always give quantitative results. Therefore we renounced the use of an extracting solution adapted to the determination of several mineral elements and chose Truog's<sup>43</sup> method for analysis of available P. It has the disadvantage of being unsuitable for the groves planted on "kurkar" soil rich in lime. On the other hand, results obtained by this method are directly comparable with those of many other workers.

### *Number of samples*

The number of samples taken from a certain grove is especially important with regard to nitrate determinations in orchard soils because of the extreme variability of nitrates under these conditions. Nitrates were determined in twenty-two separate soil samples taken at depths of 0-30 cms from an unfertilised plot of Grove A. The following results were obtained: mean—4.39 p.p.m.  $\text{NO}_3$ ; standard deviation—1.095 p.p.m.  $\text{NO}_3$ ; coefficient of variability—25%.

These variations, though considerable, are not larger than those found in fields with apparently uniform soil conditions and cultivation<sup>34,44,45</sup>. When the soil is low in nitrates, as is the case in local groves, not less than twenty separate soil samples should be taken for nitrate determination in an orchard area apparently lacking soil differences. The number should be even larger when organic manure has been applied.

The number of samples required for the determination of available P in soil was found by use of Snedecor's<sup>42</sup> formula:  $n = \frac{t^2 s^2}{(\bar{x} - m)^2}$  where  $\bar{x}$ —sample mean,  $m$ —population mean,  $s$ —standard deviation and  $t$ —according to Fisher. For determination of  $s$ , 18 separate soil samples taken from an area of about two dunams in Grove D were examined. The results in Table V indicate that eight separate soil samples suffice to obtain a representative mean for a certain grove area provided that P-fluctuations in the soil are not larger than in the examined experimental grove.

TABLE V

*Number of samples necessary to demonstrate significant differences between means for available phosphorus in the soil of Shamouti orange groves*

Available P in soil of experimental grove	Significant differences which are to be demonstrated	Required number of samples
Mean 50.5 p.p.m.	20 p.p.m.	1.6
s.d. 7.8 "	10 "	8.35
	5 "	25.8

According to the same principle, the required number of leaf samples was found to be five to eight (Table VI).

TABLE VI

*Number of leaf samples necessary to demonstrate significant differences between means for total nitrogen and phosphorus in leaves of Shamouti orange groves*

	Mean % in leaves of experimental grove	Coefficient of variability in experimental grove	Significant difference between means to be demonstrated	Required number of samples
Nitrogen	2.01	8.2	0.3 %	5
			0.2 %	8
			0.1 %	22
Phosphorus	0.147	11.1	0.03%	5
			0.02%	8
			0.01%	22



## RESULTS

Satisfactory results by diagnostic analyses may be obtained only if a suitable, well defined technique for sampling is chosen. The methods should be adapted to the examined plant, as well as to the purpose of the investigation. In the first part of our experiments, seasonal changes influencing the results of soil and leaf tests were examined, and sampling procedures were developed accordingly. In the second part of the investigations the diagnostic tests were used to estimate the nutritional requirements of orange groves.

## SEASONAL CHANGES IN SOIL AND LEAF COMPOSITION IN ORANGE GROVES

The mineral composition of soil and leaves fluctuates widely in different seasons. These changes were examined in order to ascertain the most suitable sampling season in orange groves. Non-bearing tagged twigs of the spring flush were sampled about every two months throughout the year in 2 fertiliser plots. In winter, samples from fruit-bearing twigs were also examined. Soil samples were taken simultaneously with leaf samples. The experiments were carried out for two (in some cases for three) years in Grove A. Soil phosphorus was not examined, as it is known to remain on a relatively constant level in different seasons<sup>38,22,7</sup>.

*Seasonal fluctuations of nitrates in orchard soil*

Seasonal nitrate fluctuations were nearly identical in different years. Therefore, the data of two successive years could be combined in one mean representing thirty-six separate determinations for each treatment. The results are represented in Fig. 1.

In the soil of the control plot the mean nitrogen content was low and its seasonal fluctuations small. Nevertheless these seasonal changes may be important for tree nutrition. They proved to be nearly identical in successive years. The underlying causes of the seasonal curves were not elucidated by our experiments, but a tentative explanation may be given. According to results of Russell<sup>39</sup>, Winnik<sup>46</sup>, Ettinger-Tulczynska and Elze<sup>14</sup>, we may assume that a strong seasonal increase of soil microbes produced the nitrate accumulation during the winter. This microbiological nitrate production even seems to make up for losses due to leaching during the first winter rains. A second nitrate accumulation in July-August is to be explained by environmental factors favouring decomposition of organic matter and nitrification in the irrigated soil.

In the fertilised plot the seasonal nitrate changes were dependent mainly upon the date of application and the amount of nitrogenous fertiliser used. Ammonium sulphate was applied in March and June. In March, no change in soil nitrates was found when soil samples were taken one week after application. Apparently the ammonia nitrogen had not yet been nitrified. A second analysis about 5 weeks later showed an increase of nitrates in the deeper soil layers. This may indicate

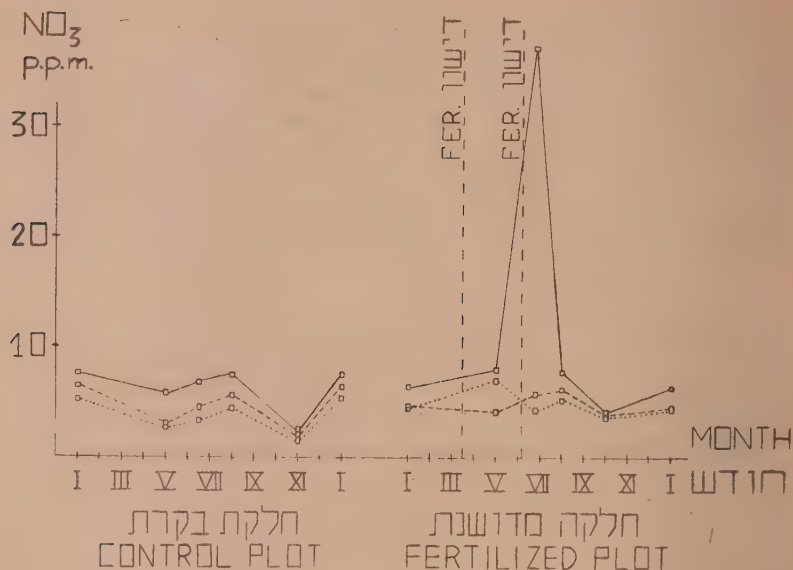


Figure 1

Seasonal nitrate fluctuations in the soil of a Shamouti orange grove

Soil level: 0—30 cms ————  
 30—60 cms - - - - -  
 60—90 cms . . . . .

that nitrates were meanwhile leached by irrigation. In June, nitrates increased considerably within one week after application of ammonium sulphate, 66 p.p.m. of nitrates were then found in a fertilised plot, as compared with 6 p.p.m. in the control. This high nitrate level in the fertilised plot persisted for some weeks only. It then decreased rapidly, and two months after fertilisation had fallen almost to the low level of the control plot. In winter, nitrate levels were even somewhat lower in the fertilised plot than in the control. This may be due to a better nitrate utilization by the well developed roots of the fertilised trees. Such an explanation is in accordance with facts reported by Schander<sup>14</sup>, Oppenheimer and Mendel<sup>32</sup>, and Albrecht<sup>1</sup>. But small differences in the mechanical composition of the soil may also be the cause of the lower N level in the fertilised plot.

Seasonal changes in nitrate levels were limited mainly to the upper 0-30 cms of the soil, and in this layer, differences among the nitrate levels of various fertiliser plots were most conspicuous. Smaller but consistent differences were found, however, even at depths of 60-90 cms.

It is not yet known if and how the periodic wetting and drying of irrigated orchard soil affects the nitrate level. Therefore soil nitrates were determined in some instances immediately before and after irrigation. Inconsistent results were obtained in different years. In the control plot, during 1946,  $\text{NO}_3$  decreased from 6.8 to 4.3 p.p.m. after irrigation, but no corresponding increase of nitrates in the

deeper soil layers was found. In 1947, there was an increase of nitrates from 6.8 before, to 10.6 p.p.m. after irrigation. This may be explained by an increase of micro-organisms when the soil is rewetted after previous drying<sup>15,39</sup>.

### *Seasonal fluctuations in the nitrogen content of leaves*

The seasonal fluctuations in the nitrogen content of leaves from various fertiliser plots were nearly parallel. Nitrogen content was lowest in leaves from the superphosphate plot due to the antagonism of N- and P- absorption. It was higher in leaves from the control plot and highest in the plots fertilised with ammonium sulphate. With adequate N supply, further nitrogen absorption was limited apparently by lack of phosphorus since in this case application of superphosphate further increased nitrogen absorption.

In young leaves a relatively low nitrogen and high phosphorus content was found (Fig. 2). During summer the nitrogen content of leaves increased gradually, reaching its maximum in August. During this period, nitrogen absorption by the tree apparently surpassed the needs of the growing organs and nitrogen was accumulated in the leaves. Afterwards there was a continuous gradual decline. It is possible that this was due to a stronger exploitation of nitrogen reserves by the growing fruit and also to increased accumulation of non-nitrogenous compounds (cellulose, lignin, minerals) in leaves. In February-March the nitrogen content of leaves decreased rapidly until it reached the same low level in all fertiliser plots. This indicates that at this period nitrogen reserves

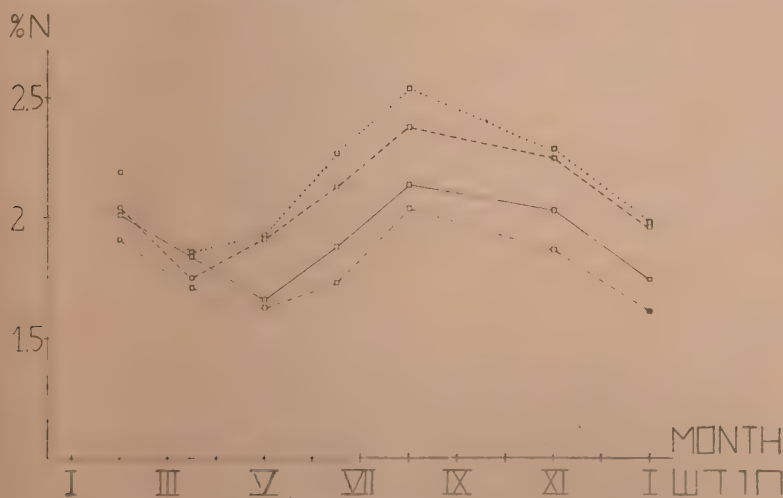


Figure 2

Seasonal fluctuations in the nitrogen content of Shamouti orange leaves

Fertiliser plots: No fertiliser ————  
 Superphosphate - - - - -  
 Ammonium sulphate .....  
 Ammonium sulphate and superphosphate . . . . .



were activated and translocated from the older leaves to the new growth flush and later to the blossoms and the young fruit. These seasonal changes of nitrogen in Shamouti leaves are concordant with those observed by Hilgeman<sup>23</sup> in grapefruit leaves but differ from results obtained by Finch<sup>16</sup> and Jones, Bitters, and Finch<sup>27</sup> in Arizona.

No definite relationship between nitrogen fluctuations in soil and in leaves could be detected in these experiments. The observed changes were parallel in spring and summer and divergent in winter. The quantitative relations between amount of nutrients in soil and absorption by the tree are obliterated under field conditions by many other factors.

#### *Seasonal fluctuations in the phosphorus content of leaves*

The phosphorus content which in young leaves is high, decreased rapidly when leaf growth stopped (Fig. 3).

During summer and fall it remained nearly constant, but there was a notable decrease in late winter. As with nitrogen, this may be explained by activation and utilization of phosphorus towards the spring growth period. Contrary to the changes in nitrogen content, however, phosphorus values did not decrease to the same low level in all fertiliser plots, but differences between plots persisted.

Table VII shows the phosphorus content of leaves more than one year old which were sampled in June. These leaves are not represented in Fig. 3. The phosphorus content of such old leaves was very low, whereas their nitrogen content was not

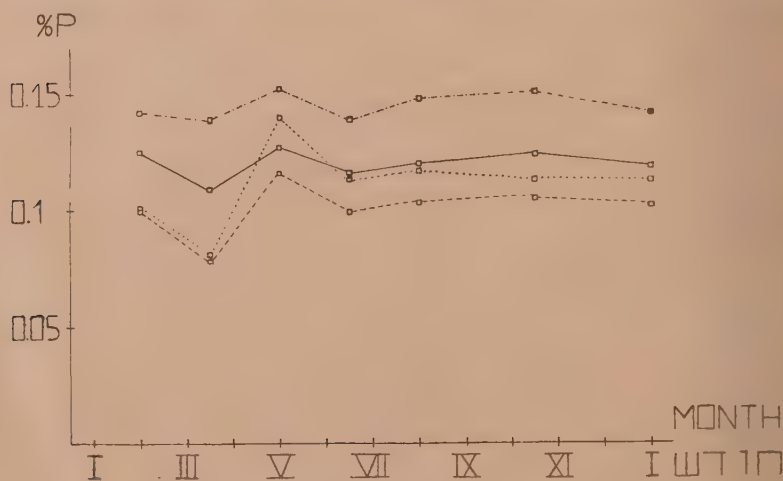


Figure 3

Seasonal fluctuations in the phosphorus content of Shamouti orange leaves

Fertiliser plots: No fertiliser

Superphosphate

Ammonium sulphate

Ammonium sulphate and superphosphate

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TABLE VII

*Phosphorus content of Shamouti orange leaves more than one year old  
sampled in June*

Fertilisation plot	Phosphorus (% of dry matter of leaves)
Superphosphate	0.109
Control	0.097
Ammonium sulphate	0.075
Ammonium sulphate and superphosphate	0.081

lower than that of one year-old leaves during the spring flush depleting them of nitrogen.

The varying phosphorus level in leaves from different fertiliser plots may be explained by the interaction of two factors: increase of the phosphorus content by superphosphate fertilisation; decrease, by application of ammonium sulphate.

#### *The suitable sampling date*

The largest differences among soil nitrate levels in different fertiliser plots were found in March-July. At this time, however, (after the main fertilisation season) it would be difficult to make adjustments in the fertiliser program of the current season according to the results of the soil test. In spring, before active root absorption begins and before fertilisers are applied, soil tests appear to be most helpful in estimating nutritional requirements of citrus trees for the current season, though the general nitrate level is low at this time.

The phosphorus and nitrogen content of citrus leaves reflect the nutritional status of the trees throughout the year except during spring flush. Differences due to fertiliser supply are most distinct in July-September. On the other hand, nutritional deficiencies are best detected in winter when leaf reserves are exhausted after ripening of the fruit.

#### THE NUTRITIONAL STATUS OF SOME SHAMOUTI ORANGE GROVES

The nutritional status of the four commercial groves in which the fertiliser experiments were carried out was examined by soil and plant analyses. These groves were chosen as representing typical fertilisation and cultivation practices in Israel citrus growing. The groves had been closely observed for six years before diagnostic tests were carried out. Here the results of chemical analyses could be compared with the former treatment of trees, with tree development, and with yields.

*Soil nitrates in orange groves*

The data represented in Table VIII indicate a low nitrate level in the soil of the examined orange groves. These values are lower than those found by several authors in other countries with similar climatic conditions<sup>19,20,26</sup>. They approach the nitrate level in the acid soils of Florida, where Bryan<sup>8</sup> found 1-3.5 p.p.m. of nitrate in soil after rain and 20-43 p.p.m. after application of nitrogenous fertilisers. Our results also agree well with those of Samuels<sup>40</sup> who considers a level of 10 p.p.m. most desirable in Californian orange groves. According to Samuels' opinion, higher quantities are not effective in increasing yields. This view is fully confirmed by our data.

TABLE VIII

*Soil nitrates in Shamouti orange groves. Sampling level: 0-30 cms.  
Season: January-February (p.p.m. of nitrates)*

Grove	Fertiliser plot	Soil nitrates
B	Control (no fertiliser)	4.35
B	Cotton seed meal	5.38
B	Cotton seed meal and superphosphate	5.02
A	Ammonium sulphate	6.21
A	Control (no fertiliser)	7.62
C	Ammonium sulphate and superphosphate	11.28
D	Ammonium sulphate and superphosphate	12.10

Significant difference 1.87 p.p.m. of nitrates

The lowest nitrate values were found in the soil of Grove B; they indicate an acute nitrogen deficiency. In this neglected grove, trees were in bad condition at the time of sampling, the twigs drying back and the leaves of yellowish colour. The soil was covered by annual and perennial weeds. It is well known that weeds seriously compete with tree roots for essential nutrients. Here the low nitrate content of the soil is to be explained, not only by continuous absorption by the citrus trees without sufficient replenishment of nitrogen reserves, but by the deteriorating effect of weeds.

In Grove A soil nitrates were somewhat higher. Here the striking differences in tree development in fertilised and control plots were not reflected by the soil nitrate status at this season. Even the fertilised soil did not contain any reserves of soluble nitrogen. The low values are characteristic of this poor sandy soil whose nitrogen reserves must be replenished annually in order to ensure normal tree growth and yields.

The highest nitrate levels were found in the soil of groves planted on loamy sand which enjoyed regular cultivation and fertilisation and yielded satisfactory returns. These values (11-12 p.p.m. of  $\text{NO}_3$ ) may therefore be designated as desirable in the soil of local orange groves.



It may be concluded that the nitrogen requirements of citrus groves can be estimated by the quantity of nitrates found in the soil of the grove, provided that all factors influencing soil fertility and nutrient absorption are carefully considered before recommendations for fertilisation are made. Moreover it should be stressed again that a representative mean of the soil nitrate status in an examined grove may be obtained only by analysis of many separate soil samples.

#### *Available Phosphorus in Citrus Grove Soils*

Most of the available phosphorus in grove soils is concentrated in the upper 0-30 cms. Phosphorus may, however, penetrate into much deeper layers if applied in solution or in holes made with a soil auger. After superphosphate application by these methods, appreciable amounts of available phosphorus were found in Grove C at a depth of 60-90 cms, whereas with the usual shallow application of superphosphate, the amounts of available phosphorus in this layer were too small for accurate determination with a du Bosque colorimeter.

The average amount of available phosphorus in the examined soils is high if evaluated by Californian standards. According to Chapman<sup>8</sup> 33-50 p.p.m. of available phosphorus provide for the needs of citrus trees and make further phosphorus fertilisation superfluous. Groves fall into three groups according to the phosphorus content of their soil in the upper layer (0-60 cms) as indicated in Table IX. A low level is indicated by values from 11.1 to 16.5 p.p.m. of available phosphorus, a medium content by 24.0-29.2 p.p.m., and a high level by 41.8-93.3 p.p.m.

TABLE IX\*

*Available phosphorus in soils of citrus groves (p.p.m. of phosphorus)*

Grove	Fertilisation	Soil level (cm)		Average
		0-30	30-60	
B	Cotton seed meal	19.0	9.2	14.1
B	Cotton seed meal and superphosphate**	20.1	4.1	12.1
B	Control, no fertiliser	24.1	8.9	16.5
C	Control, no fertiliser	33.7	14.2	24.0
D	Ammonium sulphate and superphosphate**	48.6	9.8	29.2
C	Superphosphate in holes	60.2	23.3	41.8
C	Superphosphate in solution	151.6	34.9	93.3

Significant difference between means 13.4 p.p.m. of P

Significant difference between means for soil level 7.7 " " "

\*Variations in soil phosphorus level in the plot receiving 2 kg of superphosphate in solution were much larger than in all other plots. By excluding this exceptional plot from the analysis of variance, the standard error between means was reduced from 25.73 to 9.53 p.p.m. of available P.

\*\*Shallow application of superphosphate (incorporation into the soil by hoeing).

The difference between the phosphorus levels in soils of different groves can be understood only if many interacting factors are considered; i.e., chemical and physical soil properties, kind and amount of phosphorus fertiliser used, method of its application, cultivation and irrigation of the grove, general fertiliser scheme, etc. Yet the dominant influence in the examined groves was the application of superphosphate.

An apparent deviation from this rule was observed in the neglected Grove B. Here the same phosphorus content was found in the soil of the control plot and in the plot receiving superphosphate applications two years before these studies were carried out. We assume that in the fertilised plot the available added phosphorus was completely utilized by trees and weeds.

Even the lowest values of available phosphorus found in Grove B do not indicate an acute P-deficiency. According to Chapman's<sup>9</sup> standard they would appear somewhat lower than desirable. No symptoms of phosphorus deficiency were detected in trees growing on these soils, and yields were not increased by phosphorus fertilisation.

In the more fertile soils an ample phosphorus supply was found and phosphorus fertilisation seems unnecessary for the time being. In Grove C the level of available phosphorus was high and even excessive after application of superphosphate in solution. This accords with results of Ravikovitch<sup>3,5</sup> and Ravikovitch and Lachover<sup>3,6</sup>.

We may conclude that the amount of available phosphorus in orchard soils as determined by the Truog<sup>4,5</sup> method, reflects mainly the phosphorus fertilisation of the groves and the method of fertiliser application. No conclusion on phosphorus absorption and utilization by trees is possible by means of soil analyses.

The average phosphorus and nitrogen content in dry matter of leaves of various groves and fertiliser plots are given in Table X. Phosphorus and nitrogen are recorded together because of their interdependence.

We were unable to interpret the results of leaf analyses by establishing their exact correlation with tree yields. Uncontrolled and non-nutritional factors were apparently involved in the yields obtained in the experimental groves. Nevertheless, it was obvious that nitrogen is the main nutritional factor limiting yields in the examined groves. Thus, we found a high nitrogen content in leaves from Groves C and D where yields were high. On the other hand, in the neglected Grove B trees were in poor condition, and the nitrogen content of their leaves was low. The same trends were observed in Grove A. Here tree development was much poorer in the superphosphate and control plots than in the plots fertilised with nitrogen, where nitrogen content of leaves was higher. We feel justified in concluding therefore that a high nitrogen content of leaves is desirable since it indicates an ample nitrogen supply—one of the main conditions for satisfactory returns.

*Nitrogen in orange leaves*

The nitrogen content of leaves was low in all examined groves, according to the standards of Oppenheimer<sup>30</sup> and Bathurst<sup>3</sup>. These authors designate a percentage of 1.8% of nitrogen in leaves as a low level indicating nitrogen deficiency in trees.

TABLE X

*The average nitrogen and phosphorus content of leaves in Shamouti orange groves, 1946/47 (% of dry matter of leaves)*

Grove	Fertilisation	Nitrogen	Phosphorus
B	Control (no fertiliser)	1.74	0.205
B	Cotton seed meal, 3 kg	1.92	0.130
B	" " " , 5 kg	1.97	0.133
B	" " " , 5 kg and superphosphate	1.98	0.152
A	Control (no fertiliser)	1.74	0.119
A	Superphosphate	1.61	0.142
A	Ammonium sulphate	1.96	0.102
A	Ammonium sulphate and superphosphate	1.98	0.113
A	Sheep manure, ammonium sulphate and superphosphate	2.20	0.134
D	Ammonium sulphate and superphosphate	2.01	0.147
C	Control, $\frac{1}{2}$ kg of superphosphate	2.09	0.169
C	2 kg of superphosphate in holes	2.28	0.160
C	2 kg of superphosphate in solution	2.18	0.303
Significant difference for nitrogen content		0.24%	
Significant difference for phosphorus content		0.024%	

In three experimental plots the average nitrogen content of leaves was only 1.61–1.74%. Here nitrogen deficiency was manifested by visible symptoms. This deficiency had developed from continued lack of nitrogenous fertilisation or from an unbalanced phosphorus application.

In three examined plots leaves contained about 2.2% of nitrogen, thus indicating an adequate nitrogen supply. This was reflected by tree vigour, dark green leaf colour, and high yields. The groves had received regular and ample fertiliser applications for many years. All intermediate values from 1.8 to 2.2% of nitrogen in leaves are to be considered low. In orchards where such values are found, a regular and somewhat increased nitrogenous fertilisation is advisable.



In several plots fertilised with 1 kg of ammonium sulphate per tree per year leaf analyses indicated a low nitrogen status. The small quantity of nitrogen supplied by fertilisation in most Israel groves does not permit the accumulation of nitrogen reserves in trees. The leaf analyses confirm that nitrogen added by fertilisation, if not leached in part by exaggerated irrigation or rain or lost by volatilization, is in most cases completely exploited by the crop of the same year—a fact well known to practical growers. This conclusion is also reached when analytical data of successive years are compared. Results obtained in Grove A are given in Table XI, and similar results were found in all other examined groves.

TABLE XI

*Nitrogen and phosphorus content of Shamouti orange leaves in successive years  
Grove A, 1945/46 and 1946/47 (percentage of dry matter of leaves)*

Fertilisation	Nitrogen		Phosphorus	
	1945/46	1946/47	1945/46	1946/47
Control	2.02	1.74	0.131	0.119
Superphosphate	1.95	1.61	0.140	0.142
Ammonium sulphate	2.04	1.96	0.101	0.102
Ammonium sulphate and superphosphate	2.15	1.98	0.116	0.113
Sheep manure, ammonium sulphate and superphosphate	2.27	2.20	0.124	0.134
Significant difference for nitrogen content			0.141%	
Significant difference for phosphorus content			0.015%	

With an insufficient nitrogen supply there was a continuous decrease of the nitrogen content in leaves from year to year, whereas with adequate fertilisation the nitrogen status of leaves showed only cyclic changes in successive years, though larger quantities of nitrogen were removed by yields than in the control plots. This steady decrease of nitrogen in the N-deficient plots was not reflected by soil nitrates. Here the same low status was found in successive years and the deterioration of tree conditions was not revealed by the soil test.

These data allow the conclusion that the nitrogen content of orange leaves is a reliable indicator of the nitrogenous nutrition and fertiliser requirements of trees.

#### *Phosphorus in orange leaves*

Generally the phosphorus content of leaves was high in the examined orange groves. According to Bathurst's<sup>5</sup> standards, none of the determined values indicates a P-deficiency, and some of them express an excess of phosphorus. Two different

conditions were responsible for the high phosphorus content of leaves: 1) abundant phosphorus fertilisation, 2) lack of nitrogen. Actually, nitrogen deficiency was responsible for increased phosphorus percentages in most of the examined cases and, on the other hand, adequate nitrogen fertilisation accounted for the lower phosphorus values. With a relatively low nitrogen supply, the phosphorus content of leaves reflects mainly the nitrogen nutrition of the tree, and only with an ample nitrogen fertilisation does it indicate the phosphorus status. The latter case could be observed in Grove C where excessively high P-values were found after application of 2 kg of superphosphate in solution. Application of solid superphosphate increased the phosphorus in leaves to a lesser degree. The higher P-absorption here did not depress the nitrogen content, whereas a mutual dependence of both elements was seen in Grove A.

The phosphorus content of leaves appears to be a useful guide in estimating the nutritional requirements of orange trees. In the interpretation of analyses, however, the nitrogen nutrition of trees must be taken into consideration as well. Moreover, it is probable that there are similar interrelations between phosphorus in leaves and nutritional elements other than nitrogen which are as yet less known than the N-P-antagonism.

#### DISCUSSION

A definite relationship between leaf composition, grove fertilisation, and general appearance of trees was found to exist in the reported experiments. Leaf analyses may be used to ascertain that no nutritional factor will be sufficiently low to limit tree performance, but they do not allow quantitative prediction of orange yields since, in most cases, non-nutritional factors prevent the production of such maximum yields as might be obtained according to the nutrient supply of the trees. Numerous experiments with field crops and vegetables have proved that definite correlations exist between the results of leaf and soil analyses, fertilisation, and yields. These relations make it possible to predict crop response to a certain fertiliser treatment with a high degree of probability. Such correlations are, however, very difficult to establish with perennial crops and trees. Here the correlations between yields of trees, fertilisation, and leaf composition have been proved to exist mainly in cases of severe deficiency or excess of a nutritional element. In this case, a change in the percentage of the limiting nutrient in leaves is followed by a corresponding change in the *quantity of yields*. Under ordinary grove conditions, however, prediction of yields is as yet impossible as long as many factors determinating yields are unknown or not under control. Nevertheless we feel fully justified in recommending the use of leaf analyses in practical advisory work in Shamouti orange groves since an optimal nutrient supply of trees is one of the fundamental conditions for rational citrus growing.

## SUMMARY

Soil and leaf analyses were used in estimating the nutritional requirements of Shamouti orange groves in the Israel coastal plain.

Five to eight leaf samples were found to be necessary to ascertain the nutritional status of a grove area of two dunams, while twenty soil samples or more were required for an estimation of soil nitrates in the same area.

The seasonal fluctuations of soil nitrates and of the nitrogen and phosphorus content of leaves as influenced by differential fertilisation were examined. The seasonal curves indicated spring to be the best season for soil sampling. Differences in tree nutrition as reflected by leaf composition were most conspicuous in summer, whereas nutritional deficiencies were best detected in winter after ripening of the fruit.

Soil nitrate levels in groves varied from 4 to 12 p.p.m. of soil weight in the upper 0-30 cms. Nitrate values above 10 p.p.m. were found to indicate desirable orchard conditions.

Available phosphorus (Truog) in the soil fluctuated from 14 to 93 p.p.m. in the upper 0-60 cms. The phosphorus level was determined mainly by phosphorus fertilisation. Application of superphosphate in solution increased availability and percolation of phosphorus considerably.

Generally there was an inverse relationship between the nitrogen and phosphorus content of orange leaves. With an ample nitrogen supply, however, a positive correlation between both elements was observed.

In most examined groves, nitrogen content of leaves was low (about 1.8%) and indicated the need for nitrogen fertilisation. Phosphorus in leaves was generally high due to N-deficiency, but in some cases also because of P-fertilisation. Excessive P-percentages in leaves (0.3%) were found after application of superphosphate in solution.

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## ECOLOGICAL STUDIES ON EAST MEDITERRANEAN DUNE PLANTS

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## INTRODUCTION

The sand dune belt extending along the coastal plain of Eretz Israel constitutes a well defined ecological and vegetational entity. Most of the dunes are in a stage of high mobility and are not only of no agricultural use but also hinder development of the nearby agricultural lands. As far as the application of vegetational means is concerned, the problem of dune fixation is specific for each plantgeographical region. In this country a few fixation experiments have been carried out on behalf of the afforestation bodies, but without full success, mainly because the local species best fit for dune fixation have been almost entirely ignored. So much for the practical point of view. From the purely scientific aspect, the local dune vegetation and its ecology deserve special attention since this vegetation belongs to a series of desert plants of whose ecological behaviour nothing is known as yet.

*The East Mediterranean dunes and their distribution in Eretz Israel*

The coastal dunes of the east Mediterranean countries are best developed in their southern part where they comprise a longitudinal somewhat interrupted belt running from N. Eretz Israel to N. Egypt. This belt generally increases its dimensions from north to south and its greatest centres are in the surroundings of Caesarea, Rishon le Zion, Gaza, Raffah and Sinai. This account is concerned only with that part of the belt included within the Mediterranean territory of Eretz Israel, i.e. that enjoying a mild climate with winter rains ranging between 350-800 mm.

According to the character of the dunes, their ecological conditions, and their vegetation, distinction must be made between those of high and low shore lines. The former type is typical of the greater part of the dune belt while the latter is confined to the Acre Plain and to the districts south of Gaza. In the high shore districts the shore is built up of red loam layers alternating with calcareous sandstone layers. Between the very steep slope, facing the sea and covered with a particular spray-zone vegetation, and the shore line there is a narrow tidal strip almost entirely devoid of vegetation. The sand dunes on these elevated shore ridges start at a certain distance from the western edge and increase in dimensions and in-

tensity of mobility towards the east and then disappear almost abruptly. On the other hand, in the low shore coast, the dunes rise gently near the shore, and their dimensions are considerably smaller.

### *The edaphic conditions*

The substratum over which the sands are deposited vary from place to place. In the Acre Plain it is an alluvial heavy soil, in Sharon and the Shefela it is a sandy loam or a calcareous sandstone, while in the coastal plain of the Negev the sands are deposited on loess beds. Generally the sand dunes are considered a very poor habitat both in their moisture relation and in nutrient matter. While the clay-silt fractions are everywhere exceedingly low, the relations between the coarse and fine sand fraction vary considerably. Generally, however, the fine sand fraction often reaches 60-90% of the soil sample. As to the lime content, there is a gradual increase of percentage of  $\text{CaCO}_3$  from south to north (at Khan Junis 2%, Beith Lehia 3.9%, Herzlia 9.3%, Mishmar Hayam 11.2%). The high percentage of  $\text{CaCO}_3$  in the sands of Shavei Zion is due to the extraordinary local accumulation of minute shells, corallines and nullipores.

The moisture content of the dunes has been examined in the various seasons and at three depths both in the foredunes occupied by *Agropyrum junceum* of the *Sporobolus arenarius* - *Lotus creticus* association and in the rear dunes occupied by the associations of *Artemisia monosperma* - *Cyperus mucronatus* (Fig. 1).

From the figure below it is clear that in the *Artemisia* association, moisture drops to its minimum in November while it shows two minima in the zone of *Agropyrum* and *Ammophila*, one in November and the other in April, and reaches its maximum in summer. The reason for these differences no doubt lies in the fact

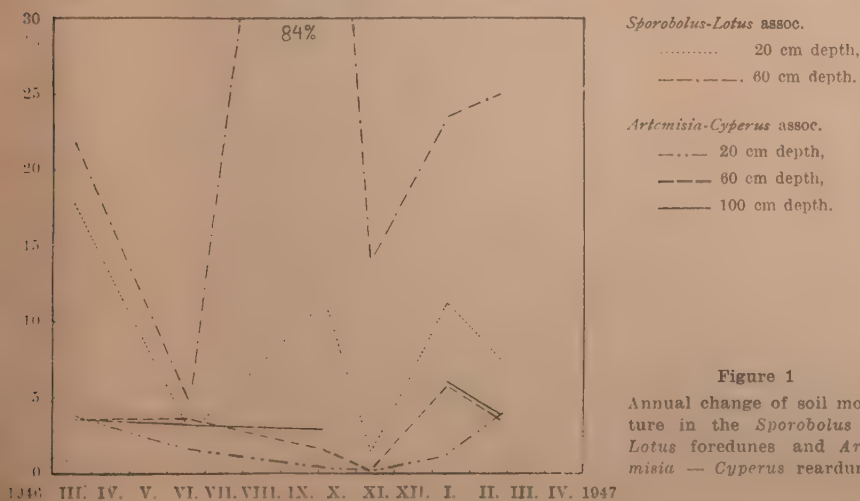


Figure 1

Annual change of soil moisture in the *Sporobolus* - *Lotus* foredunes and *Artemisia* - *Cyperus* reardunes



that the moisture of the rear dunes are conditioned by the atmospheric rainfall alone while that of the foredunes is strongly affected by tidal relations of sea water and/or ground water fluctuations at the zone nearest the sea.

The fact that the moisture content at a depth of 100 cm in the *Artemisia* zone does not exceed 5% in winter and 3% in summer shows that this amount is sufficient to support a fairly high number of comparatively flat rooted plants growing along with *Artemisia monosperma* and *Retama Roetam*. For the two latter, the roots of which penetrate to a depth of 6–20 m, these figures do not say much. As to the *Agropyrum* zone the fact that in summer a moisture amount of 84% has been observed at a depth of 60 cm shows clearly that *Agropyrum* is well supplied with moisture in the dry season. From the above examinations the conclusion can be drawn that the amount of moisture decreases considerably with the distance from the fore dunes. This refers, of course, to low shore dunes only; in the high shore dunes the relations are entirely different.

#### *The mobility of the dunes and its affect on plant life*

There is a good deal of evidence pointing to the fact that at present the coastal dunes of Eretz Israel are in a state of intense mobility. Various agricultural groves which probably have been planted on sandy clay soils adjacent to the dune belt are heavily covered up to the tops of the trees with onblown sand; houses and tracks in the vicinity of the dunes become buried deeper and deeper before ones eyes by newly forming dunes; natural maquis and forest vegetation such as associations of *Pistacia-Ceratonia*, *Quercus ithaburensis*, etc. characteristic of the nearby stable soils have been covered by sand to such an extent as to make the impression of a primary dune vegetation. This intense shifting of sand masses is no doubt the result of recent disturbances in vegetational equilibrium by man, but it is not only the eastward extension of the dunes which is striking but also the motability felt within the dune belt itself. The seasonal changes of the wind direction and its intensities introduces considerable changes in the topography of whole dune blocks, shifts the outblow centres from season to season, brings destruction in well established vegetation plots, and creates new regeneration centres of the dune vegetation.

This instability is limited mainly to the zone of the rear dunes far away from the sea shore. It is in this zone that the morphological and physiological properties of the individual dune plants are decisive both on dune formation and survival of vegetation. While in their struggle against onblow the plants must be provided with a rapid rate of upward growth of the buried shoots, the survival of the plants on the spot is chiefly dependent on the depth of the main and lateral roots and their power to maintain efficient anchorage in the soil after the entire shoot and the greatest part of the roots has been entirely exposed through outblow.

According to above properties, the leading plants of the local dune communities may be subdivided into the following three main types:

- 1) Plants able to withstand the sandcover deposited on them by means of rapid upward growing of side branches.
- 2) Plants able to withstand the removal of sand from around the roots through developing very deep roots anchoring in more compact soil layers underlying the dune.
- 3) Plants resistant to both covering and deflating wind activities.

To the first type belongs *Ammophila arenaria*, the leading plant of the *Ammophila arenaria* - *Cyperus conglomeratus* association which occupies vast stretches in the sand dune belt of Eretz Israel. It advances southwards as far as Khan Junis (near Raffah). While on low shore dunes, this association is limited to the foredunes (Acre Plain, Khan Junis) forming longitudinal ridges more or less parallel to the coastal line, in high shore dunes it is limited to rear dunes rather far away from the sea (Caesarea, Bat Yam, etc.), where irregularly scattered ridges are formed. The adventitious root system of this plant spreads horizontally under the surface of the freshly accumulated sand layers while the branching shoots push up the newly formed branches through the growing sand cover. Because of these properties, *Ammophila* is known to be an efficient dune former and sand binder. However, under vigorous wind activities directed towards removal of the accumulated sand, *Ammophila* is unable to keep its position and disappears sooner or later with the destroyed dune. To the same type belongs also *Panicum turgidum* Forsk., *Aristida scoparia* Trin. et Rupr. and others which replace *Ammophila* especially in the southern part of the dune belt. (Figs. 2 and 6).

To the second type of plants withstanding removal to a certain extent but unable to keep pace with the growing dune belongs *Agropyrum junceum* (L.) P.B. limited as elsewhere on the European coast to the front line of the foredunes.

The third type of plants withstanding both overblow of sand and removal of sand masses from around the underground shoots and roots is represented in the local dune belt by a few plants of the *Artemisia monosperma* - *Cyperus mucronatus* association. This association is most widespread along the rear dunes all along the dune belt. It appears in a few variants, and its main plants are *Artemisia monosperma* Del., *Retama Roctam* (Forsk.) Webb, *Polygonum aquisetiforme* S. et S. var. *arenarium* Eig. et Feinbr., *Tamarix pseudo-pallasii* Gutmann. *Artemisia* is an evergreen many-branched shrub, 50-100 cm high. Its main vertical root which may reach a length of 5 or more metres gives off laterals also penetrating into deep sand layers. It is not as efficient in sand binding as *Ammophila* but remains on the spot after the dune on which it was established has been entirely removed. In such cases the whole plant with the exposed parts of the roots falls down and spreads on the surface of the dune bottom, giving off new roots and shoots and so enabling the renewal of the dune.

*Retama Roctam* is another shrub with still longer roots (up to 20 m in depth

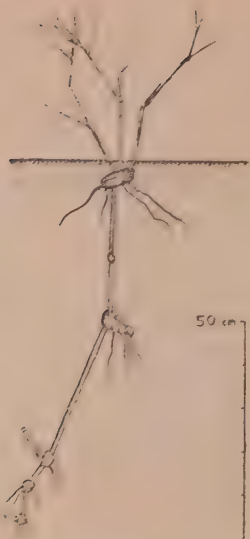


Figure 2  
*Panicum turgidum*, showing aerial shoots which after being buried by a sand layer, produced adventitious roots from their nodes



Figure 3  
*Polygonum equisetiforme* var. *arenarium*. The stem (distinguished by the inflated nodes) has been buried by a sand layer over 2 m thick. The vertical root has been only partly disclosed



Figure 4  
*Artemisia monosperma*, showing root system; the horizontal position of the revealed axis is due to falling of the plant due to outblow. Adventitious roots are produced from one of its branches

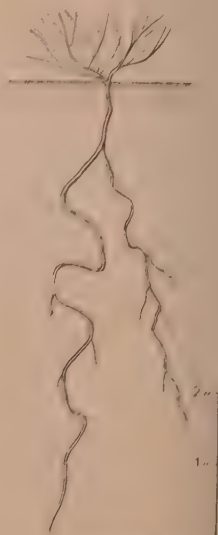


Figure 5  
*Retama Retama* showing part of the root system



Figure 6  
Part of the dune  
range inhabited by  
*Ammophila arenaria*  
(Mishmar Hayam)

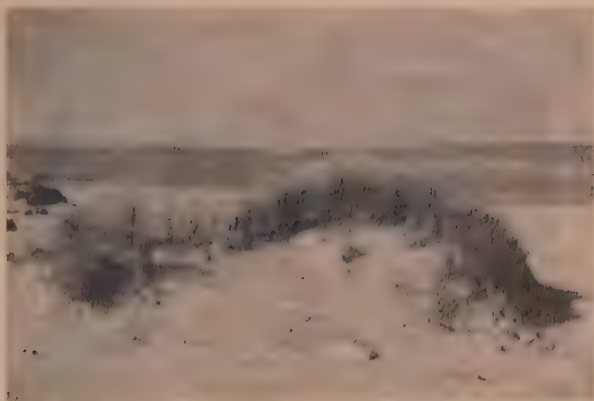


Figure 7  
Stand of *Artemisia* showing upper parts of roots barren through deflation (Mishmar Hayam)



Figure 8  
Stand of *Tamarix*  
*pseudo-pallasi* part-  
ly with exposed  
roots (a part of a  
root is held by the  
two men in the  
figure)

which is even more fit to survive dune destruction. *Polygonum* and *Tamarix pseudo-pallasii* behave similarly. The latter withstands an onblow sand cover to such an extent that entire trees buried in sand give off new shoots and roots from the trunk and crown. In the Acre Plain we have met with *Tamarix* trees entirely covered by sand, forming high hillocks from which only young twigs projected on the surface. Its roots, primary and adventitious, assumed great dimensions (over ten metres) and extended both vertically and laterally. (Fig. 3-5, 7-10).



Figure 9

*Tamarix pseudo-pallasii*, once covered by a thick sand layer up to its crown produced adventitious roots from its branches. After the removal of the sand layer through outblow, these roots became exposed and new shoots arose from the main stem (Mishmar Hayani)



Figure 10

A specimen of *Tamarix articulata* with twisted trunk and exposed roots testifying to the unstable conditions of the dunes (Sands of Holon), and the high plasticity of the plant

These four species and probably a few others are most efficient in maintaining the rear dune vegetation despite the destructive power of the wind. They no doubt deserve much attention as most efficient dune plants resistant both against on- and underblow. In fact *Artemisia* has been used in the past partly for protection of primitive vineyards and melon groves on sand soils against onblow, and *Tamarix* has recently been successfully planted in certain dune areas as a wind breaker and a dune former.

#### *Zonation of dune vegetation*

There are four main plant communities in the dune belt of Mediterranean Eretz Israel. These have been classed by Eig<sup>3</sup> under two alliances. 1) The *Lotion creticae*

comprising the *Ipomaea littoralis* - *Salsola Kali* association and the *Sporobolus arenarius* - *Lotus creticus* association. 2) The *Artemision monospermae* with the *Ammophila arenaria* - *Cyperus conglomeratus* association and *Artemisia monosperma* - *Cyperus mucronatus* association.

The above units are arranged in more or less defined belts roughly parallel to the shore line. The order of the belts, however, differs to a certain extent in the two types of the shore mentioned.

In the low shore dunes the four belts are as follows (Fig. 11):

1) The beach belt. Between the highest tide mark and the front of the fore dunes the *Salsola* - *Ipomaea* association is most characteristic. Frequent associates of *Salsola Kali* L. and *Ipomaea stolonifera* (Cyr.) J. F. Gmel. are *Cakile maritima* Scop., *Euphorbia Paralias* L., *Eryngium maritimum* L., *Euphorbia Peplus* L., etc.

This vegetation is scattered within a narrow strip of the beach belt which nowhere exceeds 100 m in breadth. Single plants of this association frequently also penetrate into the other belts.

2) The frontal fore dunes. In the front of the foredunes there is an interrupted rather narrow zone of hemmocks occupied by the *Sporobolus arenarius* - *Lotus creticus* association represented chiefly by *Agropyrum junceum* (L.) P.B. In the blowouts between the clumps of *Agropyrum* one often encounters plants of the former zone together with *Lotus creticus*, *Sporobolus arenarius* and rarely only a few plants listed by Eig<sup>1</sup> for the above association. The breadth of this belt in Mishmar Hayam does not exceed 70 m. Sometimes it is represented only by scattered plants of *Agropyrum* which do not form a belt for themselves.

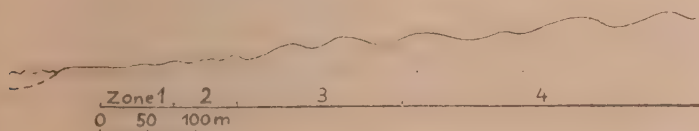


Figure 11

Schematic transect of the four belts in the low shore dunes (1. Beach belt; 2. Frontal foredunes; 3. *Ammophila* belt; 4. Reardunes)

3) The *Ammophila* belt. This belt is occupied mainly by the marram grass association, arranged along interrupted low ridges running perpendicular to the direction of the prevailing wind. This belt is rather rich in species limited to the shade of the "lees" and to outblow patches between the ridges. Among others are noted here: *Senecio joppensis* Dinsm., *Ipomaea stolonifera* (Cyr.) J. F. Gmel., *Cyperus conglomeratus* Rottb., *Atractylis flava* Desf., *Oenothera Drummondii* Hook., *Medicago marina* L., *Cutandia maritima* (L.) Bth., etc. Within this and the next belt there are isolated deep outblows covered with hydrophytic vegetation such as *Juncus acutus* L., *Scirpus Holoschoenus* L., *Phragmites communis* Trin. f. *terrestris*, etc. In Mishmar Hayam this belt reaches a width of about 200 m.

4) Rear dunes. In Mishmar Hayam this belt attains a width of about 300 m,



but it is considerably broader in other stations: The association of *Artemisia-Cyperus* is dominant here. Its coverage does not exceed 30%. Apart from *Artemisia monosperma*, *Cyperus mucronatus*, *Retama Roetam*, *Polygonum equisetiforme* var. *arenarium*, *Tamarix pseudo-pallasii* which are leading in the dune formation there are a series of other *psammophytes* inhabiting mainly culm patches. In this belt the dune dimensions and their mobility are greatest. The leading plants of this belt, as already mentioned are the most efficient dune formers as they withstand both on- and underblow.

In the high shore dune belt (as studies in the surroundings of Caesarea, Nathania, Herzlia and south of Jaffa), the following zones have been distinguished (Fig. 12):



Figure 12

Schematic transect of the high shore dune belt south of Jaffa (1. Beach; 2. Western edge of the elevated plain; 3. Shallow foredunes; 4. High reardunes)

1) The bare beach, and adjacent to it the steep slope of the elevated shore, inhabited by the *Ipomaea-Salsola* association and the *Lotus-Sporobolus* association. These are here richer in species than in the low shore dunes.

2) A strip 50–200 m broad on the western edge of the elevated plain nearest the above slope. Built up of calcareous sandstone or sandy loam, and exposed to the abrasive action of the sea wind, this strip supplies the sand blown away landwardly which accumulates and forms dunes at a certain distance from the sea. Here the association of *Atractilis flava*–*Crucianella maritima* or other associations such as littoral variants of *Thymetum capitati* or *Poterietum spinosi* etc. are most characteristic.

3) In the rear of the above zone, sand begins to accumulate into dunes increasing in height as the distance from the sea increases. In the westerly strip of this zone where the sand cover is still shallow the association of *Ononis stenophylla*–*Echium angustifolium* is most characteristic.

4) More landwards the dunes assume huge dimensions and become strongly mobile. Here the two typical dune associations, the marram grass association and the *Artemisia-Cyperus* association appear side by side; the former being confined to dunes less exposed to destruction, while the latter is dominant throughout. A considerable part of this zone is deprived of vegetation because of the extraordinary strong wind activities.

#### Factors affecting Zonation

The obvious factors responsible for the zonal arrangements of vegetation in the sand dune belt are the following:

1) The salt content of the soil nearest to the tidal mark of the beach is no doubt responsible for keeping the *Ipomaea-Salsola* association in the first front line, the *Lotus-Sporobolus* association in its rear, and the marram grass association behind both. This is also known from other investigations such as Benecke and Arnold<sup>1</sup>.

2) The degree of resistance of the individual plants to wind activities (constructive or destructive) also affects zonation. Where winds do not change their direction and strength, marram grass often holds the area once occupied. This is also the reason that in the near-to-shore belt, where the sand is too moist and heavy for wind transportation, marram grass is best established, while landwards where the sand is dry and the dunes less stable, *Ammophila* is more sporadic and limited to ridges protected against deflation.

3) A factor affecting zonation to a large extent is the sea water spray, well demonstrated by Oosting and Billings<sup>12</sup> for the dune vegetation in North Carolina.

The authors carried out two sets of experiments on the spray effect on dune vegetation using the methods of Oosting<sup>11</sup>. a) Determination of amounts of salt deposited at various distances from the sea by means of salt traps.\* b) Examinations of the degree of resistance of the main dune species to sea water spray through artificial spraying with sea water.

Of the "salt trap" experiments established several times in Mishmar Hayam (low shore dunes) and in Nathania (high shore dunes), the result of only one set for each locality are recorded here:

TABLE I

Amount of wind-borne salt at various distances from the sea in low shore dunes (in Mishmar Hayam are exposed from 17<sup>h</sup> 13.11.46 to 7<sup>h</sup> 14.11.46).

Distance from sea (m)	Amount of soluble salts on 10×10 cm cloth in mg	Vegetation
70	1.84	<i>Sporobolus-Lotus</i> association
150	0.69	<i>Ammophila</i> association
350	0.46	<i>Artemisia-Cyperus</i> association

\* On wooden frames 20×20 cm squares of cheese cloth has been stretched by means of thumb tacks. These were fixed on sticks projecting 30-40cm from the soil surface and exposed for 12-24 hours to the direction of prevailing winds at various distances from the sea shore. In the centre of the cloth a smaller square of 10×10 cm was marked and the amount of wind-borne salt deposited on these (carefully cut out from the main squares) has been determined (through solution in distilled water and titration with silver nitrate, using potassium chromate as indicator).

TABLE II

Amount of wind-borne salt at various distances from the sea in high shore dunes  
(in *Nathania*, exposed from 12<sup>h</sup> 12.11.46 to 5<sup>h</sup> 13.11.46).

Distance from sea (m)	Height (m)	Amount of soluble salts on 10×10 cm cloth (mg)	Vegetation
30	0.5	1.38	plantless beach
32	7	1.38	<i>Ipomaea-Salsola</i> association
35	15	2.53	<i>Atractilis-Crucianella</i> association
85	23	0.23	<i>Ononis-Echium</i> association

While in the low shore dunes the amount of wind-borne salt decreases considerable with the distance, in the high sea shore dunes, where the "salt traps" have been fixed at different heights of the slope the highest amount of salt was obtained on the higher terrace of the slope just near the top. From here eastwards the salt amount decreases abruptly.

Artificial spraying with sea water was given to *Agropyrum junceum*, *Ammophila arenaria*, *Artemisia monosperma*, and *Retama Roctam*. Five groups each comprising the above four species were treated for 4 days as follows: Group 1 was sprayed once daily; group 2, twice; group 3, three times; group 4, four times with sea water while the check, group 5, was sprayed four times daily with fresh water. The results obtained are as follows:

- 1) Sea water spray even when given 4 times daily showed no effect on *Agropyrum* and *Ammophila*.
- 2) In *Retama*, on the third day of the experiment, the young leaf-bearing branches started to wilt after having been sprayed two times or more daily, and on the fourth day the branches dried up entirely. On adult branches, sprays showed no obvious effect.
- 3) *Artemisia monosperma* was strongly affected by sprays. After having been sprayed twice a day for a day and a half, the leaves of the adult branches showed signs of withering, while those which were sprayed 3 and 4 times daily were withering conspicuously. After 2½ days treatment with 3-4 sprayings each day, the young shoots and the flower buds also began to suffer, and at the end of the third day all the branches sprayed 3-4 times daily dried out and died away.

The above and similar laboratory experiments carried out by Miss Lubetzky, under our supervision have clearly shown that zonation of coastal dune vegetation is largely affected by wind-borne salt water spray, and that in accordance with the degree of tolerance to salt spray, certain species keep far from the sea shore while others closely approach it. In this instance it is the fore dune vegetation which is generally unaffected by spray, whereas the dominants of the rear



dune vegetation (*Artemisia*, *Retama*, *Polygonum*) require spray-free conditions.

The above conclusions are no doubt also of practical importance in afforestation and dune fixation projects, where much attention must be paid to the tolerance of the plants to be grown to the salt spray.

### Water ecology of dune plants

Dune plants are generally classed under *xerophytes* due to the extreme edaphic and climatic conditions prevailing in their habitat, but hydro-ecological knowledge on dune plants is as yet very scant and nothing is known in the East Mediterranean countries regarding this subject. We found it, therefore, worthwhile, to collect some data on the ecology of the plants under review through transpiration measurements and examination of the osmotic values.

Of the various methods, that of rapid weighing of detached organs<sup>\*</sup> has been adopted\*. Of particular interest was the study of water output of the plants

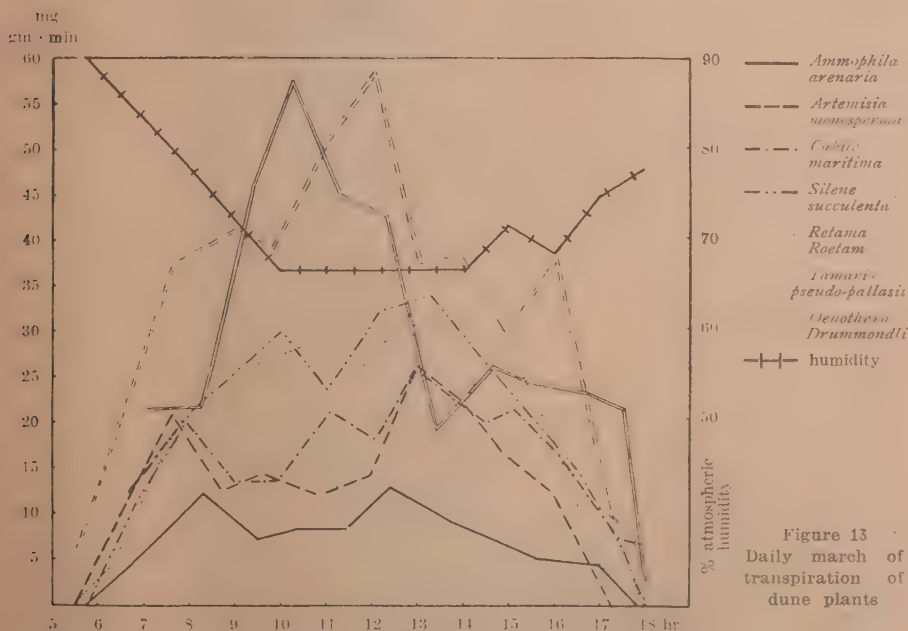


Figure 13  
Daily march of  
transpiration of  
dune plants

\* Detached leaves or parts of young green branches were weighed with the transpiration balance and exposed for 2-4 minutes; 2-4 weighings were made hourly for each transpiring organ of each species from dawn to sunset. The loss of moisture through transpiration was calculated in mg per gram fresh weight per minute (mg/gm·min). For demonstration purposes, hourly averages were also calculated. Reference to fresh weight appeared best in order to avoid difficulties involved in surface measurements which are almost impossible to carry out in the plants examined (*Ulex*, *Tamarix*, *Retama*) without significant errors. The osmotic values of cell sap were determined cryoscopically (according to Walter<sup>22</sup>). Along with transpiration measurements climatic records were collected each hour.

during the dry season. For this, measurements of a single summer day have been made since summer values of transpiration do not change greatly from day to day as do winter values. The data obtained are valid for the greater part of the summer.

The daily march of transpiration is graphically presented (Fig. 13) for *Cakile maritima*, *Artemisia monosperma*, *Ammophila arenaria*, *Oenothera Drummondii*, *Tamarix pseudo-pallasii*, *Silene succulenta* and *Retama Roetam*. These graphs show that the transpiration intensity is highest in *Tamarix* and *Oenothera* and lowest in *Ammophila*.

Most instructive are the transpiration intensity figures as calculated to mg/gm·hr and compared with figures obtained from transpiration measurement on a winter day (March).

TABLE III

Hourly transpiration intensities of dune plants on a winter and a summer day

Name	Life Form	Transpiration in mg/gm·hr		Osmotic value of cell sap September
		March	September	
<i>Tamarix pseudo-pallasi</i>	Ph	336	1020	29.1
<i>Retama Roetam</i>	NPh	264	636	21.1
<i>Artemisia monosperma</i>	Ch	476	492	23.8
<i>Oenothera Drummondii</i>	Ch	525	1250	11.7
<i>Ammophila arenaria</i>	H	—	254	16.1
<i>Silene succulenta</i>	H	258	734	12.9
<i>Cakile maritima</i>	Th	216	576	13.7

The above figures show that all *psammophytes* examined are distinguished by a transpiration intensity considerably higher in summer than in winter; some of the summer values are even 2-3 times higher than the winter values. The above transpiration figures are also in accordance with the fact that most of the dune plants show rather intense physiological activity during the summer season. The high summer values of transpiration in *Tamarix* may well be explained by the fact that this tree has extraordinarily deep roots reaching permanently moist soil layers and probably also ground water horizons. On the other hand, *Ammophila*, possessing comparatively flat roots, is a low transpirer. And yet, transpiration intensity in summer is not conditioned by root habits alone. Were it so, *Artemisia* and *Retama* with their enormously developed root systems would have shown much higher transpiration rates than they actually do.

Generally taken one can look upon Mediterranean *psammophytes* as high and medium transpirers when judging their behaviour in summer. In this regard they

differ largely from typical desert plants and flat rooted *halophytes* in which summer transpiration of 200–300 mg/gm-hr has been commonly found<sup>19,24</sup> and whose summer transpiration values are lower than the winter values. When compared with Mediterranean evergreen trees the dune plants show considerably higher summer transpiration values than *Ceratonia Siliqua*, *Laurus nobilis*, *Olea europaea*, *Pinus halepensis* in which the summer transpiration intensity does not exceed 300 mg/gm-hr.

### The osmotic values of cell sap

The osmotic values of cell sap have been determined in the following species: *Agropyrum junceum*, *Cakile maritima*, *Artemisia monosperma*, *Ammophila arenaria* and *Retama Roetam* (Fig. 14). The graphs below show a considerable drop of

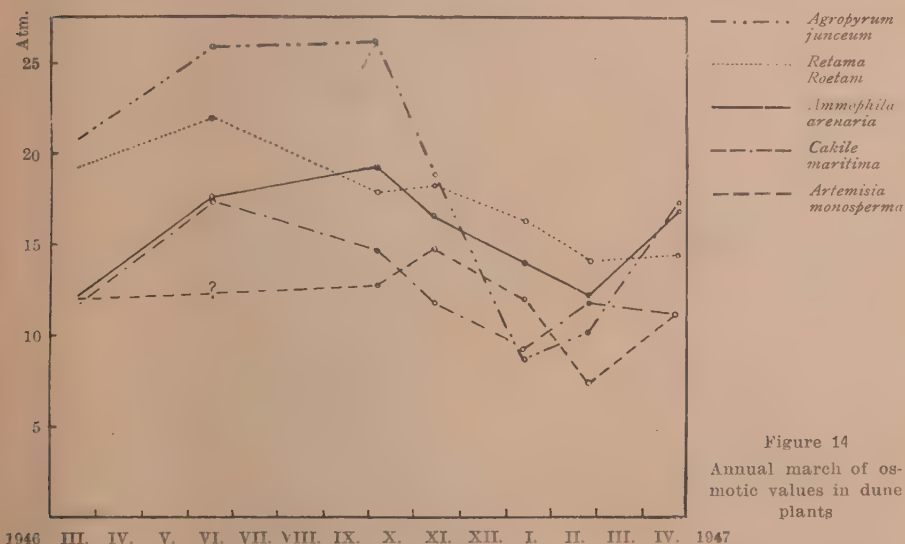


Figure 14  
Annual march of osmotic values in dune plants

the osmotic values in the winter season. While in *Cakile* and *Agropyrum* (fore dune belt), osmotic values reach the minimum immediately with the start of the rainy season, in *Ammophila*, *Retama* and *Artemisia*, the minimum values appear about one month later in the season. This can readily be explained by the fact that in the habitat of *Cakile* and *Agropyrum* the first rains are sufficient to bring about a sudden drop in the concentration of the soil solution which, as well known, directly affects osmotic values of the cell sap.

The osmotic values of sand plants are generally rather low, when compared with local *halophytes*, many of them showing summer values up to 100 atm., or with typical desert plants such as *Artemisia herba alba* and *Anabasis articulata* in which summer values exceeding 40 atm. have been found. One is led to the



conclusions that Mediterranean sand dune plants differ markedly in their water ecological behavior from both *halophytes* and desert plants. Even the succulent psammophytes such as *Cakile* and *Silene succulenta* exposed to sea water spray do not show values higher than those found in certain *hydrophytes*. The only plant showing rather higher osmotic summer values is *Tamarix* (29.1 atm.). Strangely enough we found similar values also in other species of *Tamarix* characteristic of halophytic and desert habitats. The osmotic values in *Tamarix* both in salines and in dunes do not probably reflect the moisture availability of the habitat for these plants. As a matter of fact, all the local species of *Tamarix* are exceedingly deep rooting trees and accumulate considerable amounts of soluble salts which are partly exuded and deposited on leaf surface.

## SUMMARY

1. A review of the Mediterranean sand dune vegetation of Eretz Israel has been presented, and differences have been shown between low and high shore dunes.
2. There is a gradual increase in the  $\text{CaCO}_3$  content of the dune sand from south to north. In the low shore dunes, soil moisture is greatly conditioned by the shifting of the ground water level while in the rear dune zones, precipitation alone conditions the soil moisture.
3. Observation has shown that in mobile dunes, *Ammophila* is an excellent sand binder but it is unable to survive destruction of the dune, while *Artemisia*, *Retama*, *Polygonum* and *Tamarix* resist both on- and underblow activities of the wind.
4. The amount of wind-borne salt water spray which gradually decreases in low shore dunes from west to east is to a great extent responsible for the zonation of the dune vegetation. In the high shore dunes the maximum amount of spray is precipitated on the top of the slope facing the sea, while the sand dunes starting at a certain distance from the high shore edge are almost unaffected by spray.
5. Transpiration measurements have shown that the leading plants of the dune vegetation belong to the class of high and medium transpirers.
6. Osmotic values of cell sap have been found to be considerably lower than in *halophytes* and in desert plants.

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## LES LEVURES DE LA FERMENTATION DU VIN EN ISRAËL \*†

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Je ne crois pas que le moûts de l'Etat d'Israël aient jamais fait l'objet de recherches de nature micobiologique, cela peut s'expliquer par le fait que seule une superficie très restreinte qui y est cultivée en vignes.

Mais depuis le nouvel Etat a imposé un rythme véritablement remarquable à son oeuvre de bonification et d'exploitation du sol, et que de nouvelles terres sont continuellement arrachées au désert et aux rochers, la culture de la vigne est en train de prendre une ampleur bien supérieure, et il est difficile, dans la situation présente, de dire à quel point elle s'étendra. En réalité, la production vinicole de l'Etat d'Israël est actuellement extrêmement basse, et dans tous les cas ne dépasse pas 100,000 quintaux. Mais si la production est réduite en quantité, et je pense qu'elle restera toujours dans des limites assez étroites, il existe toutefois du point de vue de la qualité certaines possibilités intéressantes. Un habitant de l'Europe méridionale, habitué de ce fait à la consommation et à la dégustation du vin est frappé, s'il se rend en Israël, par un fait : les nombreux types différents de vins qui sont obtenus grâce à la culture d'un petit nombre de variétés de vignes. Si l'on procède à une étude superficielle, il est certes facile d'en trouver l'explication dans le fait que, pour la plus grande part, les moûts sont travaillés dans deux grands établissements, qui se trouvent, peut-être, obligés de répondre aux goûts le plus disparates des citoyens israéliens venus de tous les coins du monde. Mais si l'on a eu la possibilité de goûter des produits obtenus dans de petits chais comme ceux de quelques moines français, on comprend tout de suite qu'il doit exister en Israël des conditions particulièrement favorables à la production de vins de qualité.

Etant données les conditions climatiques de la zone où se trouve Israël et la température élevée qui règne pendant la période des vendanges, on comprend de quel intérêt est une étude consacrée aux levures responsables du processus de fermentation. Aussi ai-je le désir d'exprimer mes sentiments de gratitude émue au Conseil de la Recherche Scientifique en la personne de son directeur.

\* Cette communication est extraite d'un rapport qui comprend des détails complets sur l'identification des levures, fait par Prof. Castelli au Conseil de la Recherche Scientifique, Jerusalem. Ces détails peuvent être obtenus sur demande à la Rédaction.

† Communication reçue le 31 Juillet 1951.

le professeur S. Sambursky, pour m'avoir invité en Israël afin de procéder aux recherches que j'expose ci-dessous (o).

Les recherches exécutées sur les moûts israéliens ont été menées avec le même programme que les nombreuses recherches menées depuis 1933 par l'Institut de microbiologie agricole et technique de Pérouse, et à cette fin j'avais emporté avec moi une partie du matériel nécessaire pour accomplir ces recherches.

Toutefois, avant de rendre compte des conditions techniques réunies et des résultats obtenus, je crois nécessaire de donner un bref aperçu des recherches sur les moûts italiens. En vérité, il faut reconnaître que l'étude des agents de la fermentation du vin est restée longtemps presque totalement négligée. Cela ne veut nullement dire que notamment les botanistes et également les chimistes n'aient pas exécuté de louables recherches à ce sujet, mais il s'agissait surtout d'études ayant un but d'histoire naturelle, et, ce qui a constamment fait défaut, c'est une recherche conduite systématiquement. Chacun sait qu'à la bonne qualité d'un vin concourent les facteurs les plus variés, depuis l'origine du cep jusqu'à la nature du terrain et aux procédés techniques mis en oeuvre au cours de la vinification, mais nul n'ignore non plus que c'est grâce à l'activité des levures alcooliques que le moût de raisin se transforme en vin. Il convient d'avouer qu'aussi énormes qu'aient été les acquisitions de la viticulture ainsi que de la chimie et de la technique oenologique, nos connaissances sur les agents de la fermentation du vin se réduisent à bien peu de chose. Cette opinion se trouve confirmée par l'avis exprimé par Riberau-Gayon et Genevois<sup>1</sup> dans leur récent livre "Le vin", avis qu'il faut considérer comme trop catégorique et dépourvu d'exactitude, mais certainement d'une grande valeur démonstrative. "Il n'est donc pas possible de douter qu'il existe différentes levures de vin ayant des propriétés nettement distinctes et relativement fixes et que la nature des levures possède une influence profonde sur la qualité du vin", et plus loin "En résumé, la question des levures est une des plus importantes de l'oenologie, mais tout y est à peu près inconnu; sur elle, nous savons peu de choses de plus que ce que l'on savait à l'époque de Pasteur, tant le sujet est difficile".

## 2. SEPARATION ET IDENTIFICATION DES CULTURES

Les recherches sur les agents de la fermentation du vin à partir des moûts italiens ont été commencées à l'Institut de microbiologie agricole et technique de Pérouse, par dé Rossi<sup>2</sup> pendant la vendange de 1933. Dé Rossi mit en observation 87 échantillons de moûts provenant de diverses localités de l'Ombrie. Je m'arrêterai sur ces recherches, non seulement parce que j'y ai collaboré avec un intérêt passionné, mais parce qu'elles furent à l'origine de la fixation d'une

(1) Je désire également exprimer mes remerciements cordiaux au professeur Volcani, directeur de la Station Agronomique de Rehovot et à tous ses collègues de la Station pour les facilités de toute sorte qu'ils m'ont données dans mon travail et pour la chaleureuse amitié dont ils m'ont entouré.



méthode de travail, qui est restée essentiellement identique dans les nombreuses recherches scientifiques ultérieures.

Afin d'avoir des échantillons qui correspondissent à la constitution chimique et microbiologique moyenne des produits de chacune des exploitations, les prélèvements furent pratiqués directement sur les produits venant d'être obtenus du pressurage des raisins, c'est-à-dire dans les bassines et dans les cuves. Les moûts prélevés ont été transportés de la manière la plus rapide à la quantité d'environ 1 litre par échantillon au laboratoire (o), où ils arrivaient dans les 24 heures du prélèvement, alors que généralement ils n'avaient subi encore aucune fermentation visible.

L'analyse du moût était commencée par la réalisation de préparations microscopiques que l'on colorait avec de la liqueur de Ziehl colorée, et aussitôt des bouillons de culture étaient préparés. Ces bouillons étaient réalisés par dissémination sur de la gélatine au moût de raisin qui s'est révélée la matière la plus propre à cet usage. En réalité, très rares sont les chercheurs qui utilisent ce substrat, la grande majorité préférant la gélose de malt soit telle quelle, soit additionnée de divers ingrédients. Mon expérience déjà longue de la question me permet d'affirmer catégoriquement que les substrats gélatineux sont préférables aux substrats gélosiques, et que parmi les premiers, la gélatine au moût de raisin est préférable à la gélatine de malt. Il faut dire que dans les localités où l'on produit du vin, il est très facile de se procurer du moût et de le maintenir stérile pendant longtemps. Comme le moût de raisin est très acide et que, aussi mêlé qu'il soit à la colle de poisson, il subirait pendant le réchauffement nécessaire à la stérilisation des modifications telles que le produit perdrait la capacité de se solidifier, la gélatine est préparée au moment de l'emploi en mélangeant à parties égales du moût de raisin stérile et de la gélatine à l'eau avec une concentration double (22%) de colle de poisson. Sur des tubes de moût de raisin sont faites des disséminations, et on y ajoute successivement des quantités identiques de gélatine à l'eau avec une concentration double : le substrat qu'on obtient ainsi reste solide jusqu'à la température de 24° à 25°. Les avantages que ce substrat présente pour l'étude des levures peuvent se résumer comme suit : Il se forme des colonies tout à fait caractéristiques. On a la possibilité de mettre en évidence la fluidification de la gélatine, et éventuellement son pouvoir chromogène. Ces données, qui peuvent également être d'importance au cours de l'étude d'identification, sont d'une immense portée, du fait que, dans notre cas, elles se manifestent déjà sur les plaques de culture, parce qu'elles nous permettent d'isoler les types de colonies prédominants. Trois ou quatre jours après le premier examen, c'est-à-dire quand la fermentation du moût en est déjà à sa phase tumultueuse, on refait encore une fois les analyses, et enfin, un troisième examen, exactement dans les mêmes conditions que les deux autres, est exécuté 6 ou 8 jours après le

(o) Au cours des recherches exécutées en Puglia et en Sicile les laboratoires de fortune responsables ont été équipés avec du matériel apporté de Pérouse.

début de l'opération, au moment où la phase tumultueuse de fermentation peut-être considérée comme terminée.

Sur les plaques de gélatine de moût, qui sont maintenues à une température de 16 à 18° on obtiendra cinq ou six jours après la dissémination un développement suffisant pour pouvoir procéder à l'isolement. L'isolement sera fait exclusivement sur les colonies qui, étant en nombre prédominant, représentent des espèces auxquelles il convient d'attribuer le phénomène de fermentation dans chaque échantillon de moût. Dans notre cas, il ne s'agit pas simplement de procéder à l'isolement des formes qu'on peut rencontrer dans les mouts de raisin en fermentation, mais de diriger notre attention sur les formes qui se montrent en nette prédominance. Cette notion de prédominance est obtenue soit par l'examen microscopique de moûts, soit par l'examen microscopique des colonies qui sont développées sur les plaques, ou encore par des examens microscopiques exécutés au moyen de préparations obtenues par impression sur la première plaque d'isolement de chaque échantillon. Les types de colonies peuvent être divers, mais ne sont jamais en très grand nombre. Il est logique que des colonies presque semblables puissent appartenir à des levures qu'il faut rattacher à des espèces et des genres différents et, dans ce cas, la réalisation de préparation par impression est de la plus grande utilité. Sur la première plaque de chaque échantillon qui ne peut servir pratiquement à l'isolement par suite de sa richesse excessive en colonies, on laisse tomber une lamelle couvre-objet à laquelle on fait subir une légère pression; on elevent cette lame, en colorant avec extrême prudence, et en laissant sécher à l'air, on réussit souvent à obtenir des colonies parfaitement homogènes. Ayant obtenu, par l'examen microscopique des colonies qui se sont développées sur les plaques, la notion de types prédominants, on passe alors à l'isolement des cultures. Pour chaque échantillon de moût, et pour chacune des trois analyses effectuées, on exécute 3-4-5 isolements ou parfois encore davantage. C'est cette partie de la recherche qui, comme il est clair, conditionne tout le reste des opérations et qui, autant que possible, doit être dirigé sur place.

A la Station de Rehovot, j'ai exécuté cette première phase de la recherche sur 11 échantillons de moûts. Les isolements étaient faits sur des tubes contenant de la gélose de malt inclinée, et à mon départ d'Israël j'ai pu emporter avec moi 163 cultures pures de levure provenant de l'analyse répétée à trois reprises de 11 échantillons de moût.

L'identification des cultures isolées a été effectuée à Pérouse, dans mon Institut.

On peut affirmer avec un légitime orgueil qu'aujourd'hui, aussi bien en ce qui concerne la marche à suivre dans le travail d'identification des levures, qu'en ce qui concerne les arrangements systématiques à prendre, il existe entre les chercheurs du monde entier un accord qu'on peut considérer comme proche de la perfection. Ce n'est pas le but du présent travail de donner un aperçu critique des procédés employés actuellement, mais il est évident que ceux qui ont été élaborés par l'école hollandaise de Kluywer et décrits dans les monographies de Stelling-

Dekker<sup>3</sup> sur les levures sporigènes, celles de Lodder<sup>4</sup> sur les asporigènes non filamenteux et de Lodder et Diddens<sup>5</sup> sur les asporigènes filamenteux sont appliqués d'une manière presque universelle.

### 3. RESULTATS

Le tableau ci-dessous donne la liste des espèces isolées avec les indications relatives au nombre des moûts où leur présence a été décelée et le nombre total des cultures obtenues.

ESPECES :	MOUTS :	CULTURES :
<i>Saccharomyces ellipsoideus</i> Hansen	10 sur 11	48
<i>Hanseniaspora Guilliermondi</i> Pijper	10	46
<i>Saccharomyces Chevalieri</i> Guilliermond	9	11
<i>Saccharomyces Mangini</i> Guilliermond	7	12
<i>Kloeckera apiculata</i> (Rees) Janke	6	10
<i>Hanseniaspora apulienensis</i> Castelli	4	9
<i>Saccharomyces oviformis</i> Osterwalder	4	7
<i>Saccharomyces oviformis</i> var. <i>bisporus</i> Castelli	2	2
<i>Candida Kruzei</i> (A. Castellani) Berkhout	2	2
<i>Saccharomyces carlsbergensis</i> var. <i>valdensis</i> (Osterwalder) Dekker	1	1
<i>Torulopsis Molischiana</i> var. <i>liquefaciens</i> Luparini	1	1
<i>Candida Brumptii</i> (Langeron et Guerra)	1	1
<i>Saccharomyces muciparis</i> Beijerinck	1	1
<i>Saccharomyces Chevalieri</i> var. <i>Lindneri</i> (Guill.) Dekker	1	1
<i>Saccharomyces uvarum</i> Beijerinck	1	1
<i>Saccharomyces globosus</i> Osterwalder	1	1
<i>Saccharomyces odessa</i> Schnegg et Oehlkers	1	1
<i>Saccharomyces unisporus</i> Joergensen	1	1
<i>Saccharomyces microellipsoideus</i> Osterwalder	1	1
<i>Candida lipolytica</i> (Harrison) Diddens et Lodder	1	1
<i>Saccharomyces exiguus</i> (Rees) Hansen	1	1
<i>Zygosaccharomyces Nadsoni</i> Guilliermond	1	1
<i>Saccharomyces tubiformis</i> Osterwalder	1	1
<i>Torulopsis colliculosa</i> (Hartmann) Saccardo	1	1
<i>Saccharomyces</i> sp.	1	1

Les résultats qui se dégagent de la description générale et notamment de ce tableau sont des plus démonstratifs. Il est évident que les espèces qui sont presque toujours présentes dans les moûts, sont celles à qui est dû le développement de la fermentation. Il s'agit donc de *Sacch. ellipsoideus*, *Hanseniaspora Guilliermondi*, *Sacch. Chevalieri*, et, encore dans une mesure plus réduite, de *Kloeckera api-*

*culata*, *Hanseniaspora apuliensis* et *Sacch. oviformis*. Toutefois, il convient d'observer que la fermentation de moûts israéliens doit être attribuée surtout à deux espèces qui, pratiquement (<sup>1</sup>), ont toujours été décelées dans les moûts et dont le rôle est particulièrement remarquable, à savoir le *Sacch. ellipsoideus* et l'*Hanseniaspora Guilliermondi*. Le nombre total des cultures isolées a été pour ces deux espèces respectivement de 48 pour le *Sacch. ellipsoideus* et de 46 pour l'*Hanseniaspora Guilliermondi*. La présence d'autres espèces, décelées dans deux ou même un seul échantillon de moût, doit être considérée comme une indication purement fortuite. Dans les recherches faites en Israël, on est frappé par le grand nombre des espèces isolées, mais cela ne doit être compris que très relativement puisque, pour chaque échantillon de moût, trois analyses ont été effectuées et que pour chacune d'elles un nombre considérable d'isolements ont été exécutés. Du reste, tout en restant fidèle, dans les présentes recherches, à l'idée de veiller à l'isolement des formes qui étaient en nette prédominance, j'ai été porté à faire aussi des isolements sur des colonies qui se caractérisaient par leur nature atypique. En fait, me trouvant dans une région si différente de l'Italie, j'ai cru opportun de faire une étude sur les agents de la fermentation du vin, mais en même temps, de ne pas perdre l'occasion qui m'était offerte, de conduire également une recherche qui pouvait avoir de l'importance du point de vue de l'histoire naturelle. Et c'est à cet ordre d'idées qu'appartient l'étude de l'échantillon du moût de Cabernet qui, comme nous l'avons vu, a manifesté un comportement parfaitement anormal.

Le coup d'oeil le plus fugitif sur le tableau fait ressortir avant tout un fait : les espèces décelées appartiennent, pour la plus grande part, à des formes susceptibles de produire des spores. Quel que soit l'aspect morphologique des cellules : sphériques, elliptiques, allongées, apiculées, leur classement systématique les place au nombre des levures sporigènes. En fait, sur 163 cultures isolées au total, 147 appartiennent à des espèces sporigènes et seulement 16 des espèces non susceptibles de produire des spores. Si l'on s'en tient maintenant aux cultures de forme apiculées, on remarque que 54 d'entre elles appartiennent à des espèces sporigènes du genre *Hanseniaspora*, alors que 10 seulement sont à ranger dans le genre *Kloeckera*, non sporigène.

Dans les moûts israéliens, la mise en marche de la fermentation est due presque exclusivement à des levures de forme apiculée mais celles-ci appartiennent, pour la plus grande majorité, à des espèces sporigènes du genre *Hanseniaspora*, qui se trouvent dans tous les échantillons et en quantité considérable. Une fois passé le stade de la fermentation tumultueuse, les levures de forme pointue per-

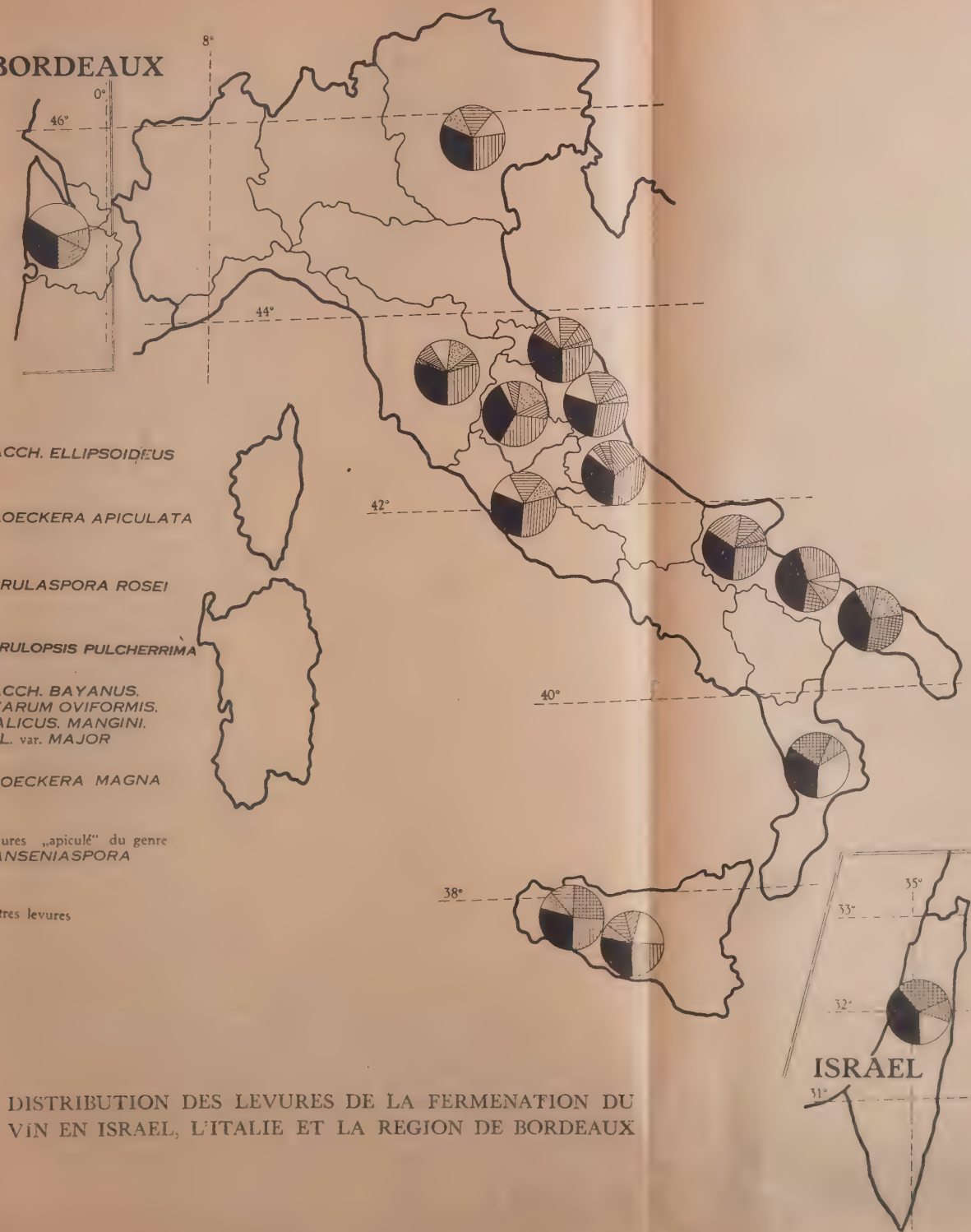
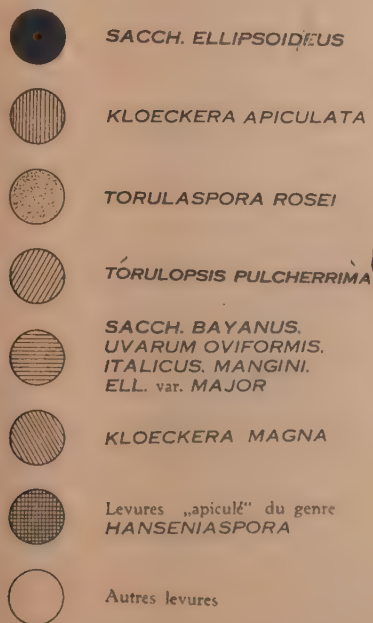
(<sup>1</sup>) Le moût de Cabernet, a manifesté un comportement parfaitement anormal au cours de sa fermentation. Que ce soit parce que la bouteille utilisée pour le prélèvement du moût n'avait pas été nettoyée ou pour une autre raison inexplicable, il reste en tout cas que cet échantillon de moût n'est entré en fermentation que pendant la huitième journée, et les plaques recueillies ont montré un développement de colonies toutes extrêmement semblables entre elles. Il aurait mais j'ai cru utile de les rapporter cependant, uniquement pour être complet.



dent du terrain et l'on voit apparaître, les levures de forme sphérique, ovale et elliptique, qui finissent par dominer nettement. Parmi ces dernières formes, la grande majorité des cultures isolées appartient à l'espèce *Sacch. ellipsoideus*, qui existe dans tous les moûts et dont on a obtenu en tout 48 souches. On ne peut considérer comme étrangères au développement de la fermentation des moûts israéliens les espèces *Sacch. Chevalieri* et *Sacch. Mangini*, décelées respectivement dans 9 et dans 7 des 11 moûts examinés, ni, quoique dans une plus petite mesure, le *Sacch. oviformis* décelé dans 4 moûts. Les autres espèces, décelées dans 1 ou 2 moûts, représentent des indications purement fortuites. Ce qui est intéressant, surtout du point de vue des applications pratiques, c'est que dans tous les moûts examinés la flore blasomycétique décelée se trouvait dans des conditions suffisantes pour assurer l'obtention de vins normaux.

Pour pouvoir confronter les résultats obtenus en Israël et ceux qu'ont mis en évidence les nombreuses recherches menées en Italie, il est nécessaire que je résume brièvement possible ces derniers. Les résultats des recherches exécutées dans les diverses régions d'Italie peuvent apparaître comme comprenant d'une part ceux qui ont été obtenus dans les zones centrales et septentrionales et d'autre part ceux qui ont été mis en évidence en Italie méridionale et en Sicile. Dans les zones centrales de l'Italie, on a décelé en général de nombreuses espèces, et les levures apiculées, appartenant à des espèces diverses, se classaient toujours parmi les formes non sporigènes du genre *Kloeckera*. La mise en marche de la fermentation était due presque toujours à des formes pointues qui, en général, pendant le cours de la fermentation, cédaient la première place à des espèces sporigènes appartenant notamment au genre *Saccharomyces*. Parmi les espèces appartenant au genre *Saccharomyces*, c'était le *Sacch. ellipsoideus* qui dominait nettement. Toutefois, dans de nombreux moûts on observait, avec des pourcentages assez considérables, d'autres espèces aussi bien sporigènes que non sporigènes, c'est-à-dire capables de produire des quantités notables ou limitées d'alcool, et dont l'intervention dans le développement naturel et normal de la fermentation ne pouvait être exclue. Il s'agit ici des espèces *Sacch. Bayanus*, *Sacch. uvarum*, *Torulaspora Rosei*, *Kloeckera magna* et *Torulopsis pulcherrima*. En Italie méridionale et en Sicile par contre, les résultats sont très différents. Par rapport aux observations faites dans la partie centrale et septentrionale de la péninsule italienne, on remarque un nombre beaucoup plus limité d'espèces, qui pour la plus grande partie, sont à ranger parmi les blastomycètes susceptibles de produire des spores. Au contraire de ce qui a été observé dans le nord, dans l'Italie du Sud et en Sicile tous les moûts présentent une microflore blastomycétique suffisante pour obtenir des vins ayant les caractères considérés comme normaux dans ces zones. En Italie du sud et en Sicile, ce sont aussi les levures pointues qui engagent la fermentation, mais elles appartiennent principalement aux sacharomycètes à classer dans le genre *Hanseniaspora* plutôt qu'aux levures asporigènes du genre *Kloeckera*. A ce point de vue, il est très intéressant de considérer ce qui se passe dans la région de la Puglia qui

# BORDEAUX



DISTRIBUTION DES LEVURES DE LA FERMENTATION DU VIN EN ISRAEL, L'ITALIE ET LA REGION DE BORDEAUX



s'étend sur une longueur considérable : tandis que dans le nord de cette région, le développement de la fermentation rappelle celui des zones centrales de l'Italie et où pourtant toutes les levures pointues sont du genre *Kloeckera*, les choses changent quand on observe le phénomène dans les autres zones de la Puglia. Dans la partie centrale, les levures isolées sont principalement sporigènes et les formes pointues appartiennent soit à des formes non sporigènes du genre *Kloeckera* soit à des formes sporigènes du genre *Hanseniaspora*. Enfin, dans le sud de la Puglia, les formes isolées sont presque toutes sporigènes et de même on constate que les levures de forme pointue sont à classer presque exclusivement dans des espèces du genre *Hanseniaspora*. Il est hors de doute que cet état de fait est dû au climat. On a recueilli en Sicile et en Calabre des résultats identiques à ceux qui ont été mis en évidence dans le centre et le sud de la Puglia.

Les résultats obtenus en Israël concordent parfaitement avec ce qui a été mis en évidence en Italie méridionale et insulaire, et particulièrement avec ce qui se passe dans la Puglia du sud. Du reste, le climat d'Israël n'est guère différent de celui de la Puglia du sud, de la Sicile et de la Calabre, et dans ces dernières régions il en est où vendange commence à la seconde décade du mois d'août.

Outre le *Sacch. ellipsoideus* et les levures pointues du genre *Hanseniaspora*, on rencontre en Israël, dans une proportion importante, le *Sacch. Chevalieri*, le *Sacch. Magnini* et le *Sacch. oviformis*, en ce qui concerne le *Sacch. Magnini*, il n'a été décelé en quantités considérables que dans les moûts siciliens, tandis que le *Sacch. Chevalieri* et surtout le *Sacch. oviformis* se sont toujours trouvés, avec une densité inférieure, un peu partout. Dans les moûts israéliens, on n'a jamais décelé la *Torulaspora Rosci*, saccharomycète dont la présence s'est manifestée avec une densité importante, dans toutes les zones italiennes. A l'instar de ce qui a été observé dans la Puglia méridionale, en Sicile et en Calabre, on n'a pas rencontré dans les moûts israéliens de *Torulopsis pulcherrima*. Dans la carte dessinée, on trouvera indiqués les diverses recherches effectuées et les résultats obtenus.

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## A DYNAMIC MODEL FOR THE FLUCTUATION OF POPULATIONS OF THE LEVANTE VOLE (*MICROTUS GUENTHERI* D.A.)

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### I. INTRODUCTION

The aim of the following analysis is to construct a model describing the population dynamics of the Levante vole as observed in Israel. Breedings since 1934, supplemented by a certain amount of field observations, supplied a considerable amount of data on the natality and mortality of that vole. Even if this material is still too small to permit refined physiological and ecological interpretation, it definitely suffices for the construction of physiological life-tables to a first approximation.

In addition, the data on fertility make possible the calculation of age distribution in a stationary vole population living under laboratory conditions where decimation by enemies, diseases, etc. occurring in nature must be neglected. This stationary vole population permits the computation of what rate of destruction is necessary in nature for the size of the vole population to remain constant. Field statistics for over ten years by Bodenheimer<sup>1</sup> indicated the extent of the seasonal and the secular fluctuations of these populations in nature. Within this frame of observations a suitable dynamic model was described. In agreement with observations and experiments by Bodenheimer and Sulmann<sup>2</sup>, the growth of the vole population was ascribed to a temporary increase in fertility. The change of the natality-factor  $K$  from 1 to 2 or 1.5 induced changes in the size and age-structure of the previously constant population. Recent observations on the breakdown of an outbreak could be similarly interpreted by a corresponding temporary decrease of the natality rate.

The analysis of these problems necessitated the constant use of mathematical methods. Yet it would have been premature to apply any subtle mathematical method or any refined methods of population analysis and renewal theory. Simplifying assumptions were made in order to facilitate the computations. Nevertheless, the evidence tends to show that our conclusions conform reasonably well with the state of affairs in nature. A more elaborate study and statistical analysis will have to be postponed till further material is gathered.

The results of the present study are compared with those of a similar one by Leslie and Ranson<sup>3</sup> of the related vole *Microtus agrestis* in the British Isles. That species with its short life-expectation, its interrupted fertility during winter and

\* Received June 1951.

the resulting small numbers of voles at the start of the reproductive period in spring, is so different from the Levante vole with its much greater longevity and fertility, that important ecological conclusions can be drawn by the comparison of the two species.

It will be noted that certain figures differ from those given in the preliminary publication of Bodenheimer<sup>1</sup>. These differences are due to changes in presentation and in the revision of certain basic data. To the former belongs the change of the  $p(a)^*$  value from the post-weaning period to the number of live-born individuals. To the latter belongs the shift of the starting age of reproduction from 40 to 60 days. The most important addition is the analysis of the effect of reduced or temporarily interrupted fertility on the vole populations; observations had shown that this is at least one important mechanism of the critical breakdown of vole outbreaks.

The writers wish to acknowledge the assistance given by Mr. A. Kogan and Mr. U. Gamsu in the computation of the tables.

## II. A GLANCE AT THE RAW STATISTICAL DATA

Table I shows the physiological longevity of the vole. It is based on a laboratory vole population of 80 individuals. These individuals were chosen at random from among a group of young voles surviving to the age of 50 days. They were henceforth kept under observation until their natural (or, in a few cases, accidental) death.

TABLE I

Year	Died during the year			Living at end of year	Percentage living at end of year	Percentage dead at end of year
	Males	Females	Total			
First	14	16	30	50	62.5	37.5
Second	5	11	16	34	42.5	57.5
Third	9	11	20	14	17.5	82.5
Fourth	7	4	11	3	4	96
Fifth	1	1	2	1	1	99
Sixth	1	0	1	0	0	100
Total	37	43	80			

The oldest female died at an age of 1398 days, while the male of greatest longevity survived till the age of 1961 days.

The minimum age of fertility is 25 days for the female vole and 35 days for the male, but in nature the first copulation and pregnancy occur a few weeks later. The gestation period is 21 days. The earliest weaning time is 10 days after birth, but in nature it is usually delayed for about a week.

\* See page 66.

The average number of voles per litter in the different months of the year is shown in Table II. This table is based on observations conducted for eight years and comprising approximately 2000 individual births.

TABLE II

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Yearly average
Average number of young per litter	5.9	6.3	6.1	6.3	6.5	6.4	4.5	5.3	4.9	4.5	5.4	5.3	5.5
Total number of litters	22	35	38	37	18	27	23	26	23	31	36	26	28.5

Thus, under laboratory conditions, the natality rate is affected only moderately by the season of the year.

Dr. M. Dor has collected valuable field data about the natural predation upon the vole population by its main bird of prey in this country, the barn owl (*Tyto alba*). The study of several thousands of pellets of the barn owl yields important information on the age distribution of the vole population in nature. Whenever the *Microtus* population is scanty, other small rodents and shrews are responsible for the majority of bones found in those pellets. On the other hand whenever *Microtus* is fairly abundant, the large majority of these bones are *Microtus* bones<sup>4</sup>. Eleven groups of 50 pellets each from various localities in the country were studied, and the age distribution of the 550 voles devoured by the barn owls was determined. The age determination was based on the weight of the lower jaw. The results are contained in the following table:

TABLE III

*Age distribution of voles devoured by barn owls*

Weight of lower jaw (mg)	80	120	160	200	240	280	320
Corresponding age of vole (days)	25	35	50	70	100	150	over 180
Locality: Be'er Tuvia	1	5	13	14	9	6	2
Gedera	0	3	8	19	12	6	2
Bet Alpha	1	5	14	14	8	5	3
Giv'oth Zaid	0	2	11	8	10	17	2
Giv'oth Zaid	1	0	5	21	14	5	4
Tiberias	0	10	17	10	2	4	7
Tiberias	0	2	15	23	7	2	1
Tiberias	0	3	5	18	17	2	5
Y'sod Hama'aloh	7	11	7	5	7	10	3
Y'sod Hama'aloh	1	6	13	22	5	2	1
Tel Khay	0	5	21	16	7	1	0
Total	11	52	129	170	98	60	30
Percent	2	9	23	31	18	11	5

It is seen from the table that only 16% of the voles devoured by the barn owl survived to an age exceeding a quarter of a year, while only 5% attained the age of half a year. Moreover, these percentages reflect the size in nature of the adult vole population only, since the subterranean habitat of the neonates protects them from strong predations by owls, as evidenced by the fact that only 2% of the devoured voles were at an age of less than one month. More than half the voles devoured by the barn owl belong to the age group of 40 to 80 days.

These empirical data agree fairly well with the general conclusions drawn from this model, thus providing a certain support for our assumptions.

### III. THE MODEL.

The simplest approach has been used in treating population problems. Even though the population and its various strata are discrete, these numbers have been treated as continuous variables. This is, of course, a justified approximation when large populations are considered. Furthermore, only expected values have been treated, and any deviation from these expected values due to a random distribution are ignored. The model is thus deterministic, which again is a justified simplification.

#### A. THE DEMOGRAPHIC FUNCTIONS

The following customary notations have been used:

$c(a)$  denotes the coefficient of age distribution; i.e. in a population of  $N$  individuals there are  $Nc(a)da$  individuals between the ages of  $a$  and  $a+da$  days.

$b$  denotes the average natality rate per individuum per day; i.e. in the above population of  $N$  individuals there are  $Nb$  new ones born per day.

$d$  denotes the average mortality rate per individuum per day; i.e. in the above population  $Nd$  is the expected number of deaths per day.

$r$  denotes the rate of natural increase per individuum per day. It is connected with  $b$  and  $d$  through the relation

$$r = b - d. \quad (1)$$

$p^+(a)$  denotes the probability, at birth, of an individuum reaching the age of  $a$  days; i.e.  $Mp(a)$  is the expected number of those among  $M$  newly born individuals that will survive to an age of  $a$  days.

$m(a)$  denotes the birth rate per individuum per day; i.e.  $M$  females at the age of  $a$  days give birth, on the average, to  $2Mm(a)$  new individuals. (The factor 2 is brought in to take account of the male population. The male and female populations are assumed to be equal in size and age distribution.)

In a population of fixed age distribution the following relations hold:

$$c(a) = b e^{-ra} p(a), \quad (2)$$



asserting that the individuals which are now at the age  $a$  were born  $a$  days ago and survived till now;

$$b \int_0^{\infty} e^{-ra} p(a) da = 1, \quad (3)$$

states that the present population is composed of all individuals born in the past and surviving till the present;

$$\int_0^{\infty} e^{-ra} p(a) m(a) da = 1, \quad (4)$$

expresses the fact that the total natality is the sum of the births at the various age groups;

In the subsequent development we base our calculations on the female part of the vole population.

#### B. CALCULATION OF $p(a)$

Before computing  $p(a)$  we have to evaluate the mortality rate  $q$ . The physiological mortality rate  $q(a, b)$  for female voles is computed as follows: If there live  $a$  female

TABLE IV  
*Rate of Mortality.*

$a$	$b$	$\alpha$	$\beta$	$\gamma$	$q(a, b)$
0	15	1037	866	*	0.191
15	30	866	665	5	0.007
30	60	665	470	5	0.009
60	90	470	345	7	0.017
90	120	345	264	1	0.003
120	150	264	216	11	0.045
150	200	216	161	5	0.026
200	250	161	118	11	0.076
250	300	118	91	6	0.056
300	350	91	78	3	0.034
350	400	78	64	8	0.107
400	450	64	58	3	0.048
450	500	58	54	2	0.035
500	600	54	40	7	0.139
600	700	40	35	0	0.000
700	800	35	24	6	0.185
800	900	24	18	5	0.213
900	1000	18	14	4	0.222
1000	1500	14	12	12	0.923

\* Since there is no  $\gamma$  for the period 0-15 days,  $q(0, 15)$  was computed as the ratio  $2 \cdot 398 / (1021 + 1037 + 837 + 866 + 398)$ . Here 1021 and 866 are the numbers corresponding to  $\alpha$  and  $\beta$  (for  $a=0$ ,  $b=15$ ) for the male population, and 398 is the number of voles, both male and female, which died from natural causes during the first 15 days.

voles at the age of  $a$  days, if all of them are observed for the next  $b-a$  days, and if during this period there occurred  $\delta$  deaths due to natural causes (and no other deaths), then  $q(a,b)$  is given approximately by  $q(a,b) = \delta/a$ .

Unfortunately, this simple procedure cannot be applied since the majority of voles under observation in our laboratory did not die natural deaths but were killed for experimental purposes. Under these circumstances we had to compute  $q(a,b)$  by means of the formula

$$q(a,b) = \frac{2\gamma}{a + \beta + \gamma},$$

where  $a$  denotes, as before, the number of female voles alive at the age of  $a$  days;  $\beta$  is the number of those among them that survived to the age of  $b$  days and  $\gamma$  is the number of those among these voles that were observed to die by natural causes during the intervening period of  $b-a$  days (Thus  $a-\beta-\gamma$  voles were killed for experimental purposes during the period under consideration).

In Table IV,  $q(a,b)$  is computed in the manner explained above from data compiled in the laboratory, starting with 1037 live-born female voles. The fluctuations in the  $q$  column are to a large extent due to the fact that only a small minority of the voles died natural deaths.

It should be noted that there is also a considerable proportion, namely about 13.6%, of still-born voles. These have naturally not been taken into account in  $q(0,15)$ , but should be borne in mind in connection with the natality rate,  $m(a)$ .

An approximate calculation of  $p(a)$  is now easily made. We put  $p(0) = 1$  and then for every pair of numbers  $a,b$  in Table IV  $p(b)$  was computed consecutively from the formula:

$$p(b) = [1 - q(a,b)]p(a).$$

The result of this computation is given in the next table.

TABLE V  
*Experimental physiological survival rate  $p(a)$*

$a$	$p(a)$	$a$	$p(a)$	$a$	$p(a)$	$a$	$p(a)$
0	1	120	0.7802	350	0.6118	700	0.4319
15	0.8086	150	0.7452	400	0.5458	800	0.3522
30	0.8033	200	0.7257	450	0.5196	900	0.2772
60	0.7962	250	0.6705	500	0.5014	1000	0.2156
90	0.7827	300	0.6331	600	0.4319	1500	0.0166

To facilitate the computations it was assumed that  $p(a)$  has a simple functional form. Specifically it was assumed that  $p(a)$  is linear in the pre-weaning period

(0–15 days) and exponential thereafter. The linear approximation needs no explanation while the exponential one follows if a constant chance (independent of age) of a vole surviving from one day to the next, is postulated.

In precise terms we put :

$$p(a) = \begin{cases} 1 - Aa & 0 \leq a \leq 15, \\ Be^{-Ca} & a \geq 15. \end{cases} \quad (5)$$

From the value of  $p(15)$  in Table V :

$$1 - 15A = 0.8086 \text{ or } A = 0.01276.$$

Next,  $C$  is determined so that the life-expectancy at the age of 15 days according to (5) is equal to that computed from Table V. The calculation yields  $C = 0.00115$

Finally,  $1 - 15A = Be^{-15C}$  gives  $B = 0.8228$ .

Thus (5) becomes

$$p(a) = \begin{cases} 1 - 0.01276a & 0 \leq a \leq 15, \\ 0.8228e^{-0.00115a} & a \geq 15. \end{cases} \quad (6)$$

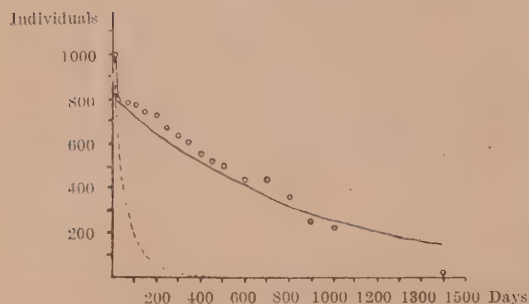


Figure 1

Survivors of 1000 live-born neonates of the Levante vole according to age: (—) of a laboratory population; ----, of a stationary and stable population in nature; oooo, of the data in Table V.

Figure 1 (unbroken line) gives a graphic representation of the function  $p(a)$  in (6); individual prints give the corresponding values read from Table V.

### C. EVALUATION OF $m(a)$ , $b$ , $r$ , AND $c(a)$

Before calculating  $c(a)$  from (2), the birth-rate  $b$  and the rate of natural increase  $r$  must be computed. The value of  $r$  can be found from (4) once the function  $m(a)$  is known.  $m(a)$  is obtained as follows: The life histories of 26 female voles are at our disposal. These histories comprise the exact periods when they were living in the same cage with a male, the dates of the various births which have occurred, and the sizes of the litters. From these data the average number of young (including still-born) per female subject to copulation per quarter of year, were computed. The results of this computation are represented graphically in the following histogram :

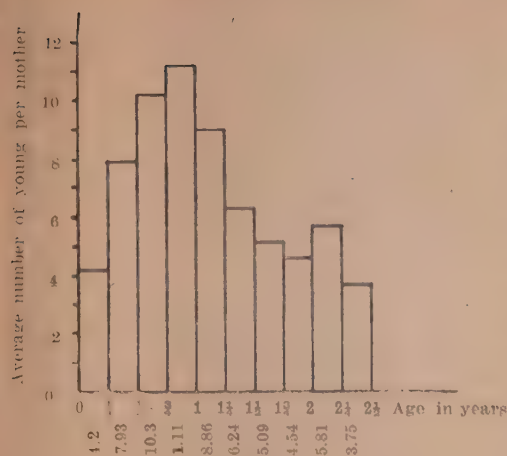


Figure 2

Fertility of the Levante vole as a function of the mother's age

This histogram shows that the fertility does not vary very strongly with the age. Apart from a highly fertile period between the ages of half a year and a year and a quarter, the natality rate is fairly constant. It seems thus not too bold a simplification to assume that  $m(a)=m$  is constant throughout the range of 60—880 days and vanishes outside this range. (The number 60 is arrived at from the data on the first copulation and the length of pregnancy given in Section II. The number 880 is more arbitrary and not very important since very few voles attain so advanced an age.)

To obtain the average  $m(a)$  for any of the time periods in Fig. 1, the corresponding ordinate must be divided by the number of days per period (i.e. 90) and by 2 (since  $m(a)$  being based on the the number of females must take only female births into account). Finally, the number thus obtained has to be multiplied by  $1 - 0.136 = 0.864$  in order to take account of the still-birth (cf. remark following Table IV). Thus the average  $m(a)$  for the second quarter year is  $0.864 \cdot 7.93 : 180 = 0.038$ . A similar calculation gives 0.0324 as the overall average of  $m(a)$ .

Since the following postulate is made :

$$m(a) = \begin{cases} 0 & \text{for } a < 60 \text{ and } a > 880, \\ m & \text{for } 60 \leq a \leq 880, \end{cases}$$

equation (4) reduces to

$$m \int_{60}^{880} e^{-\tau a} p(a) da = 1. \quad (7)$$

Taking account of (6), (7) becomes

$$0.8228m \int_{60}^{880} e^{-(\tau+0.00115)a} da = 1. \quad (8)$$

Thus, the number appearing in our computations is  $m = 0.8228 m$ ; substituting  $m = 0.0324$ ,  $m_1 = 0.0267$  is obtained. For the sake of simplicity a round number is taken :

$$m_1 = 0.03. \quad (9)$$



The higher value of  $m_i$  is also justified by the fact that the average fertility during the first year (to which period most of the vole population belongs), is greater than the overall average fertility. Such simplifications have, of course, no effect on the qualitative features of the model. Taking account of (9), equation (8) becomes

$$0.03 \int_{60}^{880} e^{-(r+0.00115)a} da = 1.$$

From this equation

$$r = 0.01227 \quad (10)$$

was easily obtained for the rate of natural increase. Substituting (6) and (10) in (3), the value

$$b = 0.01611 \quad (11)$$

was obtained for the birth-rate. Finally, from (2), (6), (10) and (11):

$$c(a) = \begin{cases} 0.01611e^{-0.01227a} (1-0.01276a) & 0 \leq a \leq 15 \\ 0.01320e^{-0.01341a} & a \geq 15 \end{cases} \quad (12)$$

is obtained for the coefficient of age distribution.

#### D. THE STABLE POPULATION OF CONSTANT SIZE

Thus far no account was taken of the vast destruction in nature. Indeed, the survival rate  $p(a)$  was assumed to be that prevailing in the laboratory population. This destruction must now be brought into consideration also. For simplicity it is assumed that over the physiological destruction there is superimposed an exponential destruction function. Thus instead of the physiological survival rate,  $p(a)$  given by (6), it was postulated that the actual survival rate,  $p_i(a)$  in nature is given by

$$p_i(a) = p(a)e^{-Da}, \quad (13)$$

$D$  being the non-physiological destruction rate.

If it is assumed that the vole population in nature has not only a stable age distribution, but is moreover of constant size, then  $D$  can easily be evaluated. Indeed, a population of constant size means  $r=0$ , thus (4) has to hold with  $r=0$  and  $p(a)$  replaced by  $p_i(a)$ . In view of (13),  $D$  has to compensate the rate of natural increase found in section IIIC. Thus from (10)

$$D = 0.01227 \quad (14)$$

is obtained.

It is very instructive to compare the expectation of life in a population with the survival rate (13) with the physiological expectation of life, i.e. when the depredations of the vole population in nature are neglected.

The physiological life-expectancy,  $V$  is defined as the average age which a vole attains before it dies a natural death.  $V$  is easily computed from the survival rate, and in our case:

$$V = \int_0^{\infty} p(a) da.$$

The life-expectation  $V_I$  in nature is similarly defined and is given by

$$V_I = \int_0^{\infty} p_I(a) da.$$

From (6), (13) and (14):

$$V = 718 \text{ days}, \quad V_I = 62 \text{ days}.$$

Thus, while under laboratory conditions a live-born vole may be expected to live two years, the life-expectancy of a live-born vole in nature hardly exceeds two months. These figures are, of course only approximate, but a glance at Tables I and III show that the conclusion drawn from our model are substantiated by observed data.

Figure 1 shows clearly the predominant part played by the non-physiological component of destruction. Indeed by a simple calculation it is found that (in a stable constant size population) about 11 times as many voles are killed by the forces of natural destruction as die due to physiological causes.

#### E. DYNAMICS OF THE VOLE POPULATION DUE TO CHANGES IN RATE OF BIRTH

In the previous section a stable and stationary vole population in nature was considered. The effect of a sudden change in the birth rate will now be treated. In the following section evidence will be presented to show that such sudden changes do occur in nature, a sudden increase in the birth rate usually preceding a vole outbreak and a sudden drastic decrease hailing the critical breakdown of such an outbreak. In the present section it will be shown that such occurrences can easily account for both the vole outbreaks and their breakdown.

Let it be assumed that there is a stable constant size vole population as described in section III D. Assume that suddenly the birth rate  $b$  given by (11) is replaced by  $Kb$ . For the sake of definiteness the case  $K > 1$ , specifically  $K=2$  will be discussed. Postulate furthermore that  $p(a)$  and  $D$ , i.e.  $p_I(a)$ , remain unchanged. It is clear that the population which has been stationary ( $r=0$ ) will start increasing in size. Furthermore, the age distribution  $c(a)$ , originally given by (12),

begins to change as a disproportionately large number of young voles enters the population. If the increased birth rate remains in force for a long period, a new stable age distribution is eventually established. The population is however not of constant size but increasing (since  $r > 0$ ). Similar phenomena occur when  $K < 1$ , i.e. when there is a drop in the birth rate.

To replace the above qualitative considerations by quantitative ones involves rather laborious calculations. The following computational procedure was used: A beginning was made with a population of 10,000 voles whose age distribution is given by (12). From (12), computations were made as to how many voles belonged to the age groups 0-20 days, 20-40 days, 40-60 days, etc. These were all considered as being of 10 days, 30 days, 50 days, etc., respectively. Then, assuming the birth rate  $Kb$  and the survival rate  $p_i(a)$ , the progeny of each of those groups as well as of the new born voles similarly treated, was followed in time-steps of 20 days each. The lengthy tables thus obtained are not reproduced; however, a portion of the information contained in them is reported here.

Table VI gives the increase in size of a stable and stationary vole population of 1000 voles in which the birth rate was suddenly multiplied by the factor  $K=2$ ; that increased birth rate remained valid for half a year, while in the following half year the birth rate reassumed its original value.

TABLE VI  
 $K=2$  for  $0 < t < 180$ ,  $K=1$  for  $180 < t < 370$

$t$	Size	$t$	Size	$t$	Size	$t$	Size
—	1000	90	2029	190	3122	290	3117
10	1245	110	2285	210	3077	310	3118
30	1422	130	2584	230	3132	330	3116
50	1558	150	2931	250	3128	350	3114
70	1778	170	3316	270	3115	370	3114

As is seen from this table, the first spur of the increased fertility resulted in an extra 245 individuals. The population then more than trebled its size within half a year of doubled birth-rate. (From the detailed table it is also seen that it was rapidly approaching a stable age distribution stage). When the birth-rate dropped to its original value the population decreased somewhat but attained quickly a state of constant-size. The effects of the half-year of increased fertility persisted however, and the size of the new population became three times the size of the initial one.

The following (Fig. 3) are histograms of the age distribution of the original population, of the population at the end of the increased fertility period and after a year. (Notice the great proximity of the first and last curves).

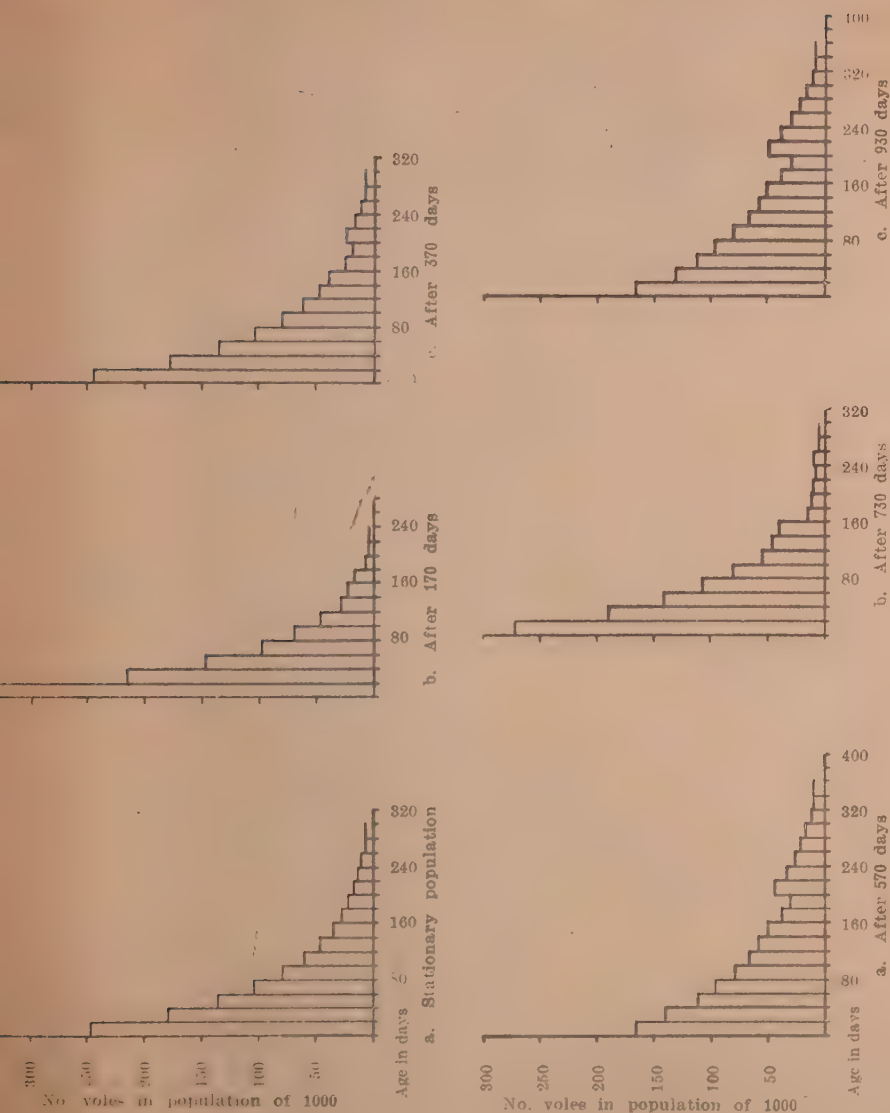


Figure 3

Age distribution in vole populations  
under the assumptions of Table VI

Figure 4

Age distribution in vole populations  
under the assumptions of Table VI a  
(continuation of Fig. 3)



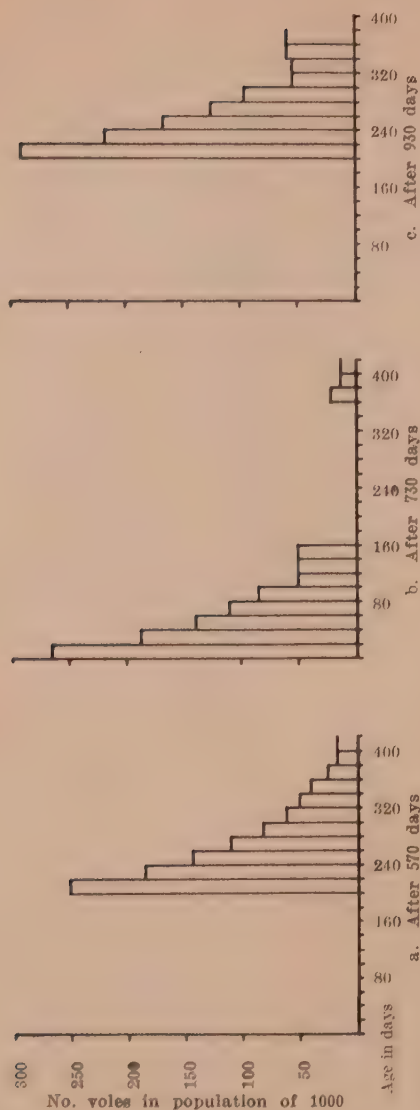


Figure 5  
Age distribution in vole populations  
under the assumptions of Table VI b  
(continuation of Fig. 3)

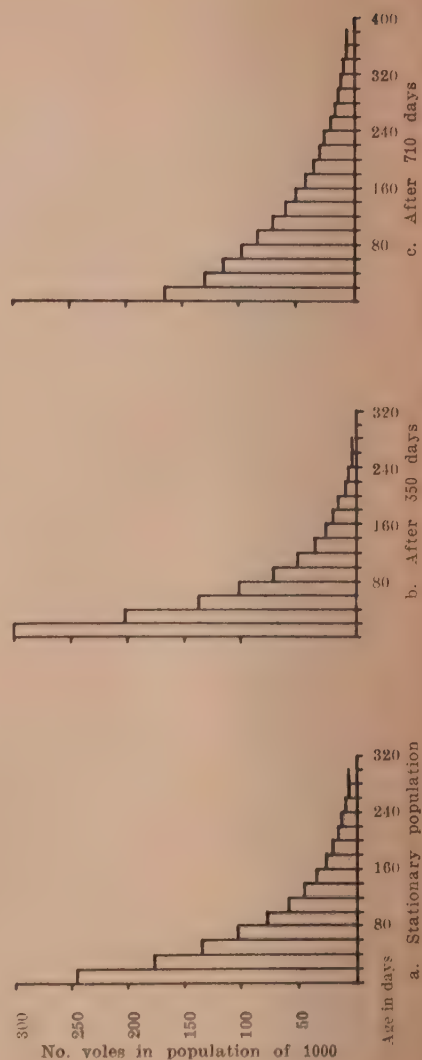


Figure 6  
Age distribution in vole populations  
under the assumptions of Table VII

The next table continues the preceeding one. It is assumed that after 380 days the birth rate suddenly falls to half its original value, stays that way for the next 200 days and then increases to 1.2 times the original value, dropping again to half the original value after 160 more days (Fig. 4).

TABLE VI a

$K=0.5$  for  $380 < t < 580$ ;  $K=1.2$  for  $580 < t < 740$ ;  $K=0.5$  for  $740 < t < 940$

$t$	Size	$t$	Size	$t$	Size	$t$	Size
390	2732	530	1363	670	1378	810	954
410	2453	550	1232	690	1413	830	865
430	2239	570	1113	710	1450	850	785
450	2031	590	1239	730	1491	870	712
470	1906	610	1289	750	1293	890	647
490	1664	630	1294	770	1150	910	585
510	1507	650	1333	790	1052	930	528

The interpretation of this table as well as of the histogram is similar to that of Table VI.

The following table is also a continuation of Table VI.

TABLE VI b

$K=0$  for  $380 < t < 580$ ;  $K=1.2$  for  $580 < t < 740$ ;  $K=0$  for  $740 < t < 940$

$t$	Size	$t$	Size	$t$	Size	$t$	Size
390	2357	530	353	670	269	810	94
410	1797	550	267	690	273	830	73
430	1373	570	202	710	279	850	56
450	1048	590	252	730	285	870	44
470	780	610	263	750	213	890	34
490	610	630	254	770	161	910	27
510	464	650	261	790	122	930	21

As will be seen in the sequel, the assumption of a complete cessation of fertility ( $K=0$ ) is by no means unrealistic. An almost complete lack of births may well be a major contributor to the disappearance of a vole outbreak. Table VIb shows clearly the rapid rate of decrease of a population in which births disappear altogether. The histogram (Fig. 5) shows the effects on the age distribution.

Finally, the case of a year of fertility increased by a factor of 1.5 and followed by a year of half the original fertility was considered.

The age distributions are shown in Fig. 6.

TABLE VII  
 $K=1.5$  for  $0 < t < 360$ ;  $K=0.5$  for  $360 < t < 720$

$t$	Size	$t$	Size	$t$	Size	$t$	Size
—	1000	—	—	—	—	—	—
10	1122	190	2086	370	3084	550	1261
30	1211	210	2235	390	2751	570	1139
50	1279	230	2395	410	2523	590	1029
70	1374	250	2567	430	2289	610	928
90	1478	270	2751	450	2071	630	837
110	1582	290	2947	470	1877	650	753
130	1694	310	3158	490	1700	670	677
150	1817	330	3381	510	1540	690	606
170	1947	350	3592	530	1394	710	542

The above tables and graphs are characteristic of the general situation. As remarked above, the approach to a stable age distribution is rather rapid, but this can be seen only from the complete tables.

#### IV. A COMPARISON BETWEEN THE POPULATION DYNAMICS OF THE BRITISH AND THE LEVANTE VOLES

The statistical analysis of the population of the British vole *Microtus agrestis* in England by Leslie and Ranson<sup>3</sup> permits an interesting comparison. This vole differs considerably in a number of highly significant ecological points from our Levante vole.

The British vole has a life-expectation of 208 days at birth, of 225 days after weaning (or slightly longer) and has a maximum (empirical) longevity of 693 days. The average number of pregnancies per female was 5 to 6 (under laboratory conditions) with 3.5 to 4.0 live births per litter. The maternal age of 80 to 200 is the most fertile period. The average physiological fertility is thus about 20 young per female.

Once its constant age distribution has become established, a vole population of these physiological constants of fertility and mortality has a rate of increase of 12.5 per thousand per day, which roughly corresponds to a power of multiplying some 10 times in six months. Under the standard conditions of diet, temperature and light maintained in the laboratory the British vole breeds continuously after having gained sexual maturity. But in nature, the winter is a non-breeding season giving the wild vole only at most a breeding season of about 182 days per annum. During the non-breeding season the physiological mortality of a stable population ranges from 46% to 66%.

Under these conditions, the annual seasonal fluctuations at the onset of spring,

causing the beginning of the breeding season to fluctuate between March and early June, must be of the highest importance. Leslie and Ranson state that unfavourable conditions causing a late start of reproduction and a higher winter mortality (these are usually coupled in nature) must bring the vole population almost to a breakdown. Highly favourable conditions, on the other hand, causing an early start of reproduction and a much reduced winter mortality, may easily give rise to a vole outbreak. They say: "The general impression left on one's mind is that of a species, which at times will of necessity fluctuate violently in numbers, owing to even comparatively small disturbances of the breeding cycle." It is conspicuous, that such sensitive populations, whilst occasionally giving rise to outbreaks under optimal conditions, run the danger of actual extinction at every prolonged period of unfavourable conditions, especially in winter and spring. A few favourable seasons, however, will permit the rapid building up of huge populations.

The corresponding data for the Levante vole are:

The mean physiological life expectation is 718 days at birth, 871 days after weaning, and it has a maximal (empiric) longevity of about 1900 days. The number of physiological pregnancies is about 13 litters per female (up to 25 having been observed) with 5 to 6 young per litter. This yields a physiological mean fertility of about 72 young per female.

A vole population of these physiological constants of mortality and fertility shows a rate of increase of 12.3 per thousand per day, once the stable age distribution has become established. This is quite near the corresponding figure for the British vole. The rate of natural destruction in a constant population is 11 times higher than the natural mortality.

Under the standard conditions of diet maintained in our laboratory, the Levante vole breeds continuously after having gained sexual maturity, with a notable reduction at high age. Fertility is always slightly decreased in the summer months. In nature reproduction is occasionally interrupted, and more or less decreased in summer.

The higher longevity, the non-interruption of the breeding season and the higher fertility should give the Levante vole an enormous advantage over the British vole. When reduced to a stable and constant population where more voles are killed by natural destruction than are dying a physiological death, this advantage is much reduced, however. The higher rate of increase is counterbalanced by a correspondingly higher natural standard destruction. But there remains the enormous advantage of the continuity of the breeding season. Obviously, environmental factors which are of such paramount importance in the British vole are of lower importance for the fluctuations of the numbers of the Levante vole. Changes in fertility caused by food, which apparently occur every year at the start of the gestation season in early winter and in early spring, are decisive in this case, especially as it seems that the length of this season of higher fertility is subject to fluctuations from year to year and that these fluctuations are decisive for the actual population



trend. But at no time are the populations of *Microtus guentheri* in Israel brought so close to the verge of destruction as are the populations of *M. agrestis*. The above advantages bring about a higher incidence and resilience of the vole population in this country.

#### V. ON THE PROBLEM OF THE CRITICAL BREAKDOWN OF VOLE OUTBREAKS

Most of our calculations deal with the mechanism of rapid vole increase leading to vole outbreaks. We have yet to discuss the problem of the crisis of such outbreaks at which the vole population is suddenly reduced from a peak to a very low density. Obviously the causes must be searched for either in changes of the natural destruction or in changes of fertility. The following deliberations describe the present state of this problem.

Enemies and diseases are the paramount factor of natural destruction. With regard to enemies, the general conclusions of Errington<sup>5</sup> that predation is only a secondary factor, apply also to voles. Observers are sometimes deeply impressed by the great number of predatory birds and that of small carnivores which assemble in an area of a vole outbreak. Apparently, however, these predators do not predate upon more than a fraction of the additional food offered by the enormously greater number of the voles. If  $n$  be the normal number of voles killed by predation in a stable population  $M$ , which may be increased to  $100 M$  at the peak of an outbreak, then  $100 n$  voles may be destroyed at that stage without having greater influence upon the increased population than  $n$  individuals destroyed normally. Actual estimates show that the effect of the assembled predators is lower than the number  $100 n$ . Thus the influence of the predators is actually lower at the peak of an outbreak than it is upon standard vole populations. When by some other reason, however, the number of voles at the peak of an outbreak is heavily reduced, the assemblage of a very large number of predators may constitute for a short time a considerable accessory factor in the sudden reduction.

With regard to diseases, our observations have given no hint so far of epidemics causing the critical breakdown of an outbreak. This is in full agreement with the authoritative statement by Elton<sup>6</sup>, that occasionally vole outbreaks may be ended by such epidemics, but that there is no reason to assume that this is the usual factor causing the crisis of outbreaks.

When the fertility is reduced to 50% ( $K = 0.5$ ), however, the population will decrease at the same rate at which an increase factor of  $K = 2.0$  will build up a sudden outbreak.

In our first survey (Bodenheimer<sup>1</sup>), we confessed ignorance with regard to the mechanism of the critical breakdown of vole outbreaks. Unfortunately, our field observations, so ably performed by Dr. M. Dor in the western valley of Jezreel, had to be interrupted from October 1948 to February 1949, a most critical period for the breakdown. Table VIII demonstrates that from June 1948 onwards fertility almost ceased in the non-irrigated lands which, of course, form by far the greatest areas

TABLE VIII

*Fertility of Microtus guentheri on irrigated and non-irrigated soils in Israel*  
1947/51

Year	Month	On irrigated soil			On non-irrigated soil		
		Females trapped non-pregnant	per month pregnant	Embryos per pregnant female	Females trapped non-pregnant	per month pregnant	Embryos per pregnant female
1947	XI	12	4	4.5	9	2	5.5
	XII	7	7	7.2	5	10	5.2
1948	I	8	11	8.5	25	5	4.6
	II	3	9	10.0	13	1	8.1
	III	—	—	—	8	21	9.2
	IV	—	—	—	18	21	9.2
	V	—	—	—	19	13	8.8
	VI	14	2	5.0	6	—	—
	VII	—	—	—	15	—	—
	VIII	—	—	—	4	—	—
	IX	—	—	—	2	—	—
1949	III	8	19	11.1	—	—	—
	IV	2	4	11.0	5	—	—
	V	1	2	10.0	16	—	—
	VI	9	2	8.0	9	—	—
	VII	4	—	—	13	—	—
	VIII	10	2	5.5	11	—	—
	IX	7	12	6.1	9	—	—
	X	2	7	6.7	10	—	—
	XI	9	6	6.3	10	—	—
	XII	9	2	9.5	8	2	7.0
	I	10	5	9.5	4	1	?
	II	3	8	10.5	2	3	9.0
1950	III	7	1	11.0	4	6	10.0
	IV	3	8	12.0	8	—	—
	V	13	6	6.7	1	—	—
	VI	10	—	—	—	—	—
	VII	10	—	—	14	—	—
	VIII	10	—	—	4	—	—
	IX	9	—	—	5	—	—
	X	—	4	7.0	5	—	—
	XI	1	9	7.5	1	3	4.7
	XII	3	12	10.0	3	—	—
1951	I	3	9	7.4	1	—	—
	II	2	12	10.1	—	—	—
	III	1	12	11.6	—	—	—
	IV	5	7	7.0	—	—	—
	V	13	—	—	—	—	—

infested by voles. There occurred a few short periods of low fertility: possibly in the winter of 1948/49 (not observed), 1949/50, and still more abortive in late 1950. Fertility on the irrigated lands showed fluctuations with winter peaks and summer lows, but showed few interruptions (perhaps in the summer of 1948, from June to September 1950, and possibly again in the summer of 1951).

Table VIII shows that the number of trapped females is not high, but this figure definitely indicates the monthly trend of fertility, at least from March 1949 onwards. Here only the data regarding fertility are given. A full interpretation of the field observations is reserved for a later publication.

The above shows that nine or more consecutive months of a most reduced fertility occur in nature. It is obvious that such a period of prolonged sterility brought about the breakdown of the 1948/49 vole outbreak in this country. Prolonged drought can be regarded as the responsible extero-stimulation. At least one type of critical breakdown is thus fully explained. Along the southern border of its area *Microtus* lives in a dangerous zone of low fertility at irregular intervals. The foregoing calculations show clearly that the observed reduction of fertility fully explains the rapid breakdown of the outbreak.

Another most important point resulting from these observations is the primary importance of the vole nuclei in moist soils (irrigated land, such as berseem fields, margins of swamps, borders of irrigation ditches, especially in heavy soil) for the survival of the species in years of drought. If the analysis is correct, a great increase of the vole danger is to be expected in the coming ascendance of our secular rain cycle, provided that other biotic or abiotic factors are not strengthened during heavier and more prolonged periods of rain, and that prolonged heavy rains will not prove fatal to the voles, especially on heavy soils.

Our dynamic model of the fluctuations of the populations of the Levante vole in Israel is certainly open to many criticisms. Further research will fill many gaps of our physiological and ecological data, but the utility of the model cannot be doubted. It permits the reconstruction of the main features in broad outline, and it provides a first glimpse at the factors inducing the outbreak as well as the critical breakdown. We do not claim this model to be valid in other regions or in all future outbreaks in this country. Nature always offers surprises to its assiduous students. Yet our progressive approach in the study of the mechanisms involved in a special problem may also be useful under other conditions or in the analysis of other biological phenomena.

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# LETTERS TO THE EDITOR

The Editorial Board does not accept responsibility for the views expressed in the letters printed below.

## NOTE ON DIMENSIONS IN TENSOR ANALYSIS \*

1. At the root of tensor-analysis are the two expressions for the linear element

$$\left. \begin{aligned} (ds)^2 &= g_{ik} dx^i dx^k = dx^i dx_i = g^{ik} dx_i dx_k \\ ds &= dx^i e_i = dx_i e^i \end{aligned} \right\} 1$$

The dimension of  $ds$  is

$$[ds] = [l] \quad (2)$$

This is compatible with either one of the three following systems:—

$$(i) \left. \begin{aligned} [g_{ik}] &= [l^2], [x^i] = [l^0], [x^k] = [l^0], [x_i] = [l^0] \\ [e_i] &= [l], [e^i] = [l^{-1}] \end{aligned} \right\} (3)$$

$$(ii) \left. \begin{aligned} [g_{ik}] &= [l^2], [x^i] = [l], [g^{ik}] = [l^0], [x_i] = [l] \\ [e_i] &= [l^0], [e^i] = [l^0] \end{aligned} \right\} (4)$$

(iii) In this system one attaches to the different  $x^i$  the dimensions of the geometrical quantities which they represent. E.g. in cylindrical coordinates  $x^1=r$  would be a length,  $x^2=\theta$  dimensionless and  $x^3=z$  again a length. Therefore both the different covariant or contravariant coordinates would have different dimensions and the base vectors such dimensions as would be required by (1.2) while the different components of either  $g_{ik}$  or  $g^{ik}$  would also have different dimensions.

2. For instance in cylindrical coordinates where

$$\left. \begin{aligned} dx^1 &= dr, dx^2 = r d\theta, dx^3 = dz \\ dx_1 &= dr, dx_2 = r^2 d\theta, dx_3 = dz \\ e_1 &= 1, e_2 = r, e_3 = 1 & e^1 = 1, e^2 = r^{-1}, e^3 = 1 \\ \left. \begin{aligned} g_{ik} &= \begin{vmatrix} 1 & 0 & 0 \\ 0 & r^2 & 0 \\ 0 & 0 & 1 \end{vmatrix} & g^{ik} &= \begin{vmatrix} 1 & 0 & 0 \\ 0 & 1/r^2 & 0 \\ 0 & 0 & 1 \end{vmatrix} \end{aligned} \right\} \end{aligned} \right\} (5)$$

we would have (measuring  $l$ , say, in centimeters)

$$\left. \begin{aligned} \text{in case (i)} \quad dx^i &= dr \text{ rad}, d\theta \text{ rad}, dz \text{ rad} \\ e_i &= 1 \text{ cm}, r \text{ cm}, 1 \text{ cm} \\ g_{ik} &= 1 \text{ cm}^2, r^2 \text{ cm}^2, 1 \text{ cm}^2 \\ dx_i &= dr \text{ cm}^2, r^2 d\theta \text{ cm}^2, dz \text{ cm}^2 \\ e^i &= 1 \text{ cm}^{-1}, r^{-1} \text{ cm}^{-1}, 1 \text{ cm}^{-1} \\ g^{ik} &= 1 \text{ cm}^{-2}, 1/r^2 \text{ cm}^{-2}, 1 \text{ cm}^{-2} \end{aligned} \right\} (6)$$

$$\left. \begin{aligned} \text{in case (ii)} \quad dx^i &= dr \text{ cm}, d\theta \text{ cm}, dz \text{ cm} \\ e_i &= 1 \text{ rad}, r \text{ rad}, 1 \text{ rad} \\ g_{ik} &= 1 \text{ rad}, r^2 \text{ rad}, 1 \text{ rad} \\ dx_i &= dr \text{ cm}, r^2 d\theta \text{ cm}, dz \text{ cm} \\ e^i &= 1 \text{ rad}, r^{-1} \text{ rad}, 1 \text{ rad} \\ g^{ik} &= 1 \text{ rad}, 1/r^2 \text{ rad}, 1 \text{ rad} \end{aligned} \right\} (7)$$

$$\left. \begin{aligned} \text{in case (iii)} \quad dx^i &= dr \text{ cm}, d\theta \text{ rad}, dz \text{ cm} \\ e_i &= 1 \text{ rad}, r \text{ cm}, 1 \text{ rad} \\ g_{ik} &= 1 \text{ rad}, r^2 \text{ cm}^2, 1 \text{ rad} \\ dx_i &= dr \text{ cm}, r^2 d\theta \text{ cm}^2, dz \text{ cm} \\ e^i &= 1 \text{ rad}, r^{-1} \text{ cm}^{-1}, 1 \text{ rad} \\ g^{ik} &= 1 \text{ rad}, 1/r^2 \text{ cm}^{-2}, 1 \text{ rad} \end{aligned} \right\} (8)$$

We have not found that any textbook except Ollendorff<sup>†</sup>, who favours system (1), is outspoken about this point, but consequences of inattention may be serious. When it is stated, as is often done, that in rectangular Cartesian coordinates the covariant and contravariant coordinates are indistinguishable, this refers in case (i) to their numerical values only, the dimensions being still different and only in case (ii) and (iii) does this include dimensions.

More serious is the following:

The tensor of infinitesimal strain is defined by Brillouin<sup>‡</sup> (p. 224) by the expression

$$2\varepsilon_{ij} = \frac{\partial g_{ij}}{\partial x^\alpha} \Delta x^\alpha - \frac{\partial \Delta x^\beta}{\partial x^i} g_{i\beta} - \frac{\partial \Delta x^\gamma}{\partial x^j} g_{j\gamma} \quad (9)$$

This gives for cylindrical coordinates:

$$\left. \begin{aligned} \varepsilon_{rr} &= \delta \Delta r / \delta r \\ \varepsilon_{\theta\theta} &= r \Delta r + r^2 \frac{\delta \Delta \theta}{\delta \theta} \\ \varepsilon_{zz} &= \delta \Delta z / \delta z \\ \varepsilon_{r\theta} &= 1/2 \left( \frac{\delta \Delta r}{\delta \theta} + r^2 \frac{\delta \Delta \theta}{\delta r} \right) = \varepsilon_{\theta r} \\ \varepsilon_{\theta z} &= 1/2 \left( r^2 \frac{\delta \Delta \theta}{\delta z} + \frac{\delta \Delta z}{\delta \theta} \right) = \varepsilon_{z\theta} \\ \varepsilon_{rz} &= 1/2 \left( \frac{\delta \Delta z}{\delta r} + \frac{\delta \Delta r}{\delta z} \right) = \varepsilon_{zr} \end{aligned} \right\} (10)$$

One will naturally assume that  $r$ ,  $\theta$  and  $z$  have the geometrical dimensions as in system (iii) and one then finds that the different co-

\* Received May 1951.



variant components of  $\varepsilon_{ij}$  have different dimensions, viz.  $\varepsilon_{rr}$ ,  $\varepsilon_{zz}$  and  $\varepsilon_{rz}$  the dimension  $[l^0]$ ,  $\varepsilon_{r\theta}$  and  $\varepsilon_{\theta z}$  the dimension  $[l^1]$  and  $\varepsilon_{\theta\theta}$  the dimension  $[l^2]$ .

This reasoning is, however, inapplicable to system (i) and (ii) because in eqs. (10) the dimensions of the unit factors  $g_{rr}$  and  $g_{zz}$  have been lost in the calculations. In these two systems where all  $dx^i$  and therefore also all  $\Delta x^i$  are of the same dimensions, eq. (9) shows that the dimensions of all  $\varepsilon_{ij}$  are the same as those of the metric tensor  $g_{ik}$ . This means that in system (i)

$$[\varepsilon_{ij}] = [l^2] \quad (11)$$

while in system (ii)

$$[\varepsilon^{ij}] = [l^0] \quad (12)$$

In both systems (i) and (ii)

$$[\varepsilon^i_j] = [l^0] \quad (13)$$

The dimensions of the contravariant tensor are in system (i)

$$[\varepsilon_{ij}] = [l^{-2}] \quad (14)$$

in system (ii)

$$[\varepsilon^{ij}] = [l^0] \quad (15)$$

while in system (iii) components again have different dimensions. In rectilinear coordinates systems (ii) and (iii) are identical, while system (i) stands apart. *As only a dimensionless number can be used as a measure of strain*, we see that only in system (ii) do there exist covariant, contravariant and mixed measures of strain. We have not found that this is noted in any of the numerous papers on elasticity which make use of tensor notation. We do not wish to express preference for any one of the systems, but to avoid misunderstandings it is desirable to state in every problem involving tensor calculations what system of dimensions has been adopted, as done by Ollendorff<sup>1</sup> for rectilinear coordinates.

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## MICRODETERMINATION OF BROMIDES\*

For an investigation of the bromide content of Israeli water sources, it was necessary to elaborate a reliable analytical method which had to take into account the very low concentration of bromide ions present.

Most methods<sup>1,2,3,4</sup> described in the literature for the semi-micro-determination of bromides in the presence of chlorides, are based on the oxidation of bromide to bromate by sodium hypochlorite in a buffer solution (boric acid, etc.). Schuele<sup>5</sup> oxidizes the bromide by chlorine water to bromine monochloride, destroying the excess of chlorine by potassium cyanide. All methods suffer from the fact that the blank value is appreciable, since even the purest commercial grades of reagents contain relatively significant quantities of bromide: Ordinary electrolytic chlorine contains 0.01–0.1% of bromine; samples of hypochlorite or chlorine water prepared from such chlorine are, therefore, also contaminated. It has now been found that through oxidation of B.P. hydrochloric acid by addition of a small quantity of permanganate in an open vessel, even the *last traces of bromine* are completely removed. The chlorine generated from such pretreated hydrochloric acid plus additional permanganate was passed into a solution of C.P. sodium hydroxide so that the final reagent solution was approximately 0.3 N in hypochlorite and 0.04 N in hydroxide.

Van der Meulen<sup>2</sup> found it useful to work in the presence of an excess of sodium chloride. In accordance with Kolthoff and Yutzy<sup>1</sup> and Brodie and Friedman<sup>3</sup> this was found superfluous and even undesirable, as it introduces a certain amount of bromide ions.

For the reduction of the excess hypochlorite, formic acid was used in preference to the previously recommended sodium formate. It was found necessary to use freshly distilled acid (25% solution).

With these precautions, accurate results were obtained: the blank values were reduced to 0.4–0.75 cc of 0.002 N thiosulphate. Assays of C.P. bromide (0.2–2.0 mg) showed a systematic error of 1.0% (800 determinations); the average difference between parallel determinations was 0.025%.

\* Received May 9, 1951.

In these experiments, no evidence was encountered for the formation of chlorate, as suggested by Schulek<sup>5</sup>. Formation of chlorate would, of course, have given too high values.

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#### MOLAR REFRACTIONS OF COLOURED SUBSTANCES \*

The comparison of observed molar refractions of organic substances with those calculated from bond refractions<sup>1</sup> is strictly justified

only if measurements are carried out at a wavelength which is sufficiently removed from that of the absorption bands of the substances. In the vicinity of such regions large divergencies between the measured and calculated molar refractions occur; these divergencies are ascribed to anomalous dispersion<sup>2</sup>. Sometimes, however, considerable exaltations of the molar refraction are observed even if the refractive index is measured with light sufficiently remote from any absorption band. Thus the value calculated for the colourless sorbic acid (I) is 27 cc, while the value observed with sodium light is 34 cc.

In such cases, one may speak of a "real" exaltation of the molar refraction, more or less independent of the wavelength.

For a determination of the nature of the exaltation of the molar refraction measured with visible light for coloured substances, i.e., substances which absorb in the visible region, two possibilities offer themselves: (i) measurement of the refractive index in the near infrared, where no absorption is likely to occur; (ii) comparison of the molar refractions, for a given visible line, of substances differing structurally, but exhibiting approximately the same colour and intensity of absorption. If the ob-

TABLE I  
Molar Refraction of Some Red Substances

Substance		$R_{\text{calc.}}^D$ (cc)	$R_{\text{obs.}}^D$ (cc)	$R_{\text{obs.}}^D - R_{\text{calc.}}^D$ (% of $R_{\text{calc.}}^D$ )
Dibiphenylene-ethylene	(II)	108 <sup>a)</sup>	139.5 ± 0.5	29
2,2'-Dibromo-dibiphenylene-ethylene		123	150 ± 1.6	22
1,4'-Dibromo-dibiphenylene-ethylene		123	165 ± 1.7	34
2,3-Diphenylindone	(III)	88.5	87.5 ± 0.5	0
Azobenzene		60.5	63.0 ± 0.4	4
4-(Benzeneazo)-1-methoxy-naphthalene	(IV)	81	94 ± 1.2	16
Rubicone	(V)	113 <sup>b)</sup>	181 ± 5	16
Isatin		38	41 ± 0.4	8
Chrysoquinone		82	81.5 ± 0.8	0
1-Methylamino-anthraquinone		71 <sup>c)</sup>	79.5 ± 2.5	(12)
Fluorenone-ketazine	(VI)	118.5 <sup>d)</sup>	128 ± 1.2	(13)
2-Chloro-3-phenyl-1-benzhydrylidene-indene	(VII)	124 <sup>e)</sup>	137 ± 3	(10)
Tetraphenyl-1,4-quinodimethane	(VIII)	138	182 ± 4	32
Tetraphenyl-1,4-naphthoquinodimethane	(IX)	154	183 ± 1.5	19
Diphenylfulvene	(X)	77	84 ± 0.5	9

a) 112, based on  $R^D$  observed for fluorene.

b) The C-C bond refraction for naphthalene (2.78) has been used here.

\* Received May 15, 1951.

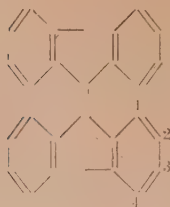
c) 78, based on  $R^D$  observed for anthracene.

d) 118, based on  $R^D$  observed for fluorene.

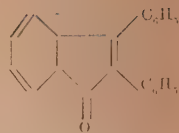
e) 133, based on  $R^D$  observed for benzhydrylidene-indene.



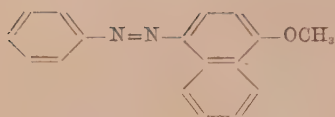
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II



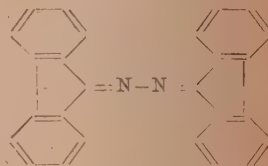
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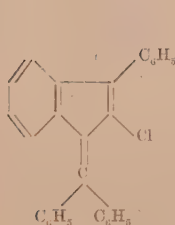
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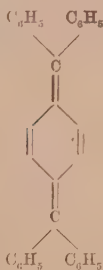
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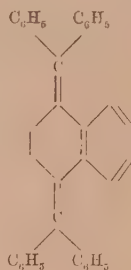
VI



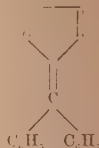
VII



VIII



IX



X

served exaltations are due to anomalous dispersion, they should have the same order of magnitude for all these compounds, independently of their specific structure, while otherwise varying degrees of exaltation should be expected.

(i) Jaffe<sup>3</sup> has recently described a method for the determination of the refractive index in the  $1\mu$  region. With this device, the molar refraction of the red dibiphenylene-ethylene (II) (longest absorption maxima at 4580, 3480 and 3080 Å)<sup>4</sup>, has been measured at  $1\mu$ ; it was  $R_{\text{obs}}^D$  136.5  $\pm$  4.5 cc, as compared with 139.5  $\pm$  0.5 cc found for the D-line (the observed values for benzene were 25.8 and 26.2 cc, respectively), whilst the sum ( $R_{\text{calc}}^D$ ) of the bond refractions (for the D-line) of this substance is about 110 cc. The large exaltation clearly continues to exist in the  $1\mu$  region. Since this method still requires comparatively large quan-

ties of material, it has not yet been applied to other substances.

(ii) The results of the second approach are summarised in Table I, which refers to red substances having absorption maxima in the region 4000–4600 Å. No obvious correlation between colour and the extent of the exaltation of molar refraction can be deduced from these figures.

Apart from its theoretical interest the existence of large "real" exaltations of the molar refraction is of paramount importance for the calculation of the dipole moment of coloured substances, especially if they possess only a small moment. The dipole moment is proportional to the square root of the difference of total polarisation and molar refraction. Therefore, if this difference is small as compared with the absolute value of the molar refraction, the latter strongly affects the value of the moment. Thus, for dibiphenylene-ethylene (II),  $P=131 \pm 1$  cc<sup>5</sup>. Using the above values

for the molar refraction, the moment is either zero (with  $R_{\text{obs}}^D$ ) or 1.1 D (with  $R_{\text{calc}}^D$ ). The latter figure would seem rather high for so symmetrical a hydrocarbon.

In a recent publication<sup>2</sup>, Sutton and co-workers ascribe any exaltations of the molar refraction of coloured substances to strong absorption in the near and ultraviolet region, and therefore advocate the calculation, in such cases, of the molar refraction from bond refractivities, for the evaluation of the dipole moment. It appears now that in many cases the exaltations of  $R^D$  for coloured substances are "real" in the sense defined above, and  $R_{\text{obs}}^D$  should be used in the calculation of the dipole moment.

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#### BENZO-HEPTAFULVENES\*

Berthier and Pullman<sup>1</sup> have studied the electronic structure of the yet unknown heptafulvene (I) molecule<sup>2</sup> and have predicted for that hydrocarbon a finite dipole moment which is directed away from the seven-membered ring. Thus, (I) only partially resembles the fulvene (II) proper. Applying the method of molecular orbitals, the benzologs (III), (IV), V, and (VI) have now been investigated. Whilst the direction of the dipole moment in (I) is not affected by the annellation, the extent of the electron transfer diminishes with the increase in size of the molecule, independently of the location of the benzene rings. The theoretical dipole moments corresponding to the substances (I) and (III)–(VI) are — 1.1, 0.6; (II): 2.8; (IV): 1.1; (V): 0.8 and (VI): 0.8 D.

It has been shown before<sup>3</sup> that this first approximation gives too high values for the moments. A successively better approximation is

obtained by the following two assumptions: (a) The Coulomb integrals are the same for all carbon atoms, but the exchange integrals of the C-C bonds vary with the mobile bond index. (b) The Coulomb integrals of the carbon atom vary with the absolute electric charges of these atoms. Thus one arrives at a moment of 0.85 D for (I). In the fulvene series, this method has given the correct value for the dipole moment of fulvene (II). Equally, a substance like (IV) would have a moment of 0.3 D.

The theory permits the further prediction that the spectroscopic characteristics of the heptafulvenes would be very similar to those of the fulvenes. In particular, the energy of the transition  $N \rightarrow V_1$  increases with increasing annellation, so that a hypsochromic effect of the annellation is expected for the longest absorption band—an effect which is reversed in passing from (IV) to (VI).

$\alpha$ -Aryl-derivatives (VII) of the 2,3,6,7-dibenzoheptafulvene (IV) have been prepared by reaction of benzylmagnesium chloride and p-chlorobenzylmagnesium chloride with 2,3,6,7-dibenzo-2,4,6-cycloheptatrienone<sup>4</sup> (VIII). (VII, R=H) is an oil, b.p. 210°/0.1 mm; (VII, R=Cl) crystallises from petroleum ether and has m.p. 155°. Their dipole moments are for R=H:  $0.2 \pm 0.2$  D, and for R=Cl:  $1.37 \pm 0.04$  D. Whilst the order of magnitude of the moment concords with the theory, it seems that its direction is rather the inverse of the theoretically predicted one. The spectrum is rather different from that of the fulvene. For (VII, R=H) and (VII, R=Cl) the following bands have been observed: 2840 Å (log  $\epsilon$ =4.90); 2280 Å (4.62) and 2850 Å (4.36); 2300 Å (4.52). The longest absorption band of benzylidene-fluorene, on the other hand, lies at 3260 Å<sup>5</sup>.

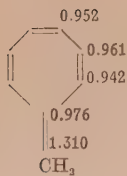
One will have to conclude that the divergence between theory and experiment stems from a factor which has not been taken into account in the calculation, viz. the possible non-planarity of the seven-membered ring. Indeed, any deviation from planarity would destroy the conjugation between the double bonds and thus obviate the predicted effects.

This conclusion is borne out by the following observations:

- (1) The tetrabenzoheptafulvalene (IX), which was prepared by reduction of (VIII) (m.p. 281°, from toluene) is colourless<sup>6</sup>.
- (2) 1-Fluorenylidene-2,3,6,7-dibenzo-2,4,6-cycloheptatriene (IX) (m.p. 255°) is a colourless substance, which resembles in its physical properties benzhydrylidene-fluorene (X).
- (3) In contradistinction with the dibenzofulvenes<sup>7</sup>, the compounds (VII) are not attacked by lithium aluminium hydride. This proves

\* Received, May 15, 1951.

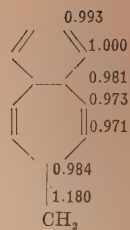




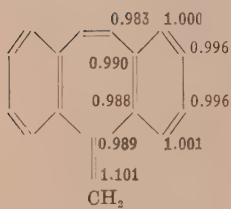
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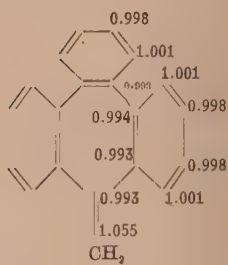
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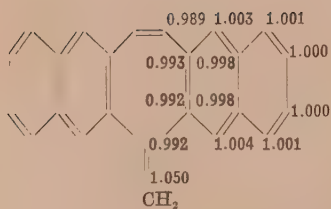
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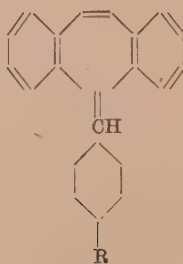
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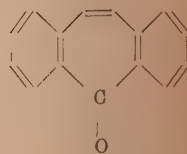
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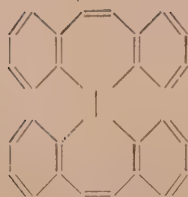
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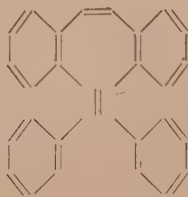
VII



VIII



VIII



IX



X

that their semicyclic double bonds are devoid of polar character.

The details of this investigation will be published elsewhere.

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#### INFRARED FREQUENCY AND POLAR CHARACTER OF CARBONYL GROUPS, ESPECIALLY IN POLYCYCLIC SYSTEMS\*

Recent calculations by the method of molecular orbitals<sup>1</sup> have revealed that the unusual character of the semicyclic double bond of the fulvenes<sup>2</sup> is reflected in the lack of polar properties in the carbonyl group of the "fulvene ketones" of the general type

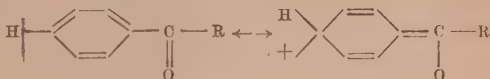


As it seems well established that the wavelength of the infrared absorption of a C=O grouping expresses the relative contribution

$$+ - 3,4,5$$

of an ionic form C=O, the infrared spectrum of the fulvene ketones and related substances appeared to offer a means for the verification of the theory. Indeed, the difference of the carbonyl frequencies of acetone or other

dialkylketones (1718–1721 cm<sup>-1</sup>)<sup>6</sup> and of a substance such as 2,6-dimethylpyrone (1671 cm<sup>-1</sup>)<sup>7</sup> illustrates this possibility: to the actual state of (I), a "benzenoid" structure (Ia) is known to contribute significantly, as indicated both by the physical and chemical properties of the substance<sup>8</sup>. It is also understandable, that aromatic (or aromatic-aliphatic) and  $\alpha$ ,  $\beta$ -unsaturated ketones show a lower frequency than aliphatic ones,



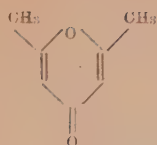
as here resonance structure will contribute markedly to the actual state of the molecule. Thus, acetophenone<sup>7,9</sup> and mesityl oxide<sup>10</sup> absorb at 1690 cm<sup>-1</sup>.

Two other structural effects have to be taken into account in an evaluation of the infrared spectra of ketones. "Crowding" of the carbonyl by alkyl groups reduces the frequency (which may be explained by the inductive (+I) effect of the groups). Thus the carbonyl frequency of acetone (1718 cm<sup>-1</sup>) appears at 1638 cm<sup>-1</sup> in hexamethylacetone<sup>11</sup>, and that of cyclohexanone (1708 cm<sup>-1</sup>) at 1684 cm<sup>-1</sup> in its  $\alpha$ ,  $\alpha'$ ,  $\alpha''$ -tetrabenzyl derivative<sup>12</sup>. Furthermore, there is a marked difference in the carbonyl frequency of cyclohexanone and cyclopentanone (1733 cm<sup>-1</sup>)<sup>7</sup>. This difference has already been commented upon<sup>13</sup> and may be due to the effects of "I-strain"<sup>14</sup>.

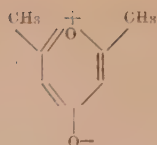
The investigation of the three "fulvene ketones" tetraphenylcyclopentadienone (II), 2,3-diphenylindone (III, R=C<sub>6</sub>H<sub>5</sub>), and fluorenone (IV) has, indeed, shown (see Table I) that in accordance with the theory, the carbonyl group in these compounds has only a low degree of polarity. It is much lower than that prevalent in benzophenone or dibenzylidene-acetone (V). This effect disappears partly in the benzoderivatives of fluorenone: 3,4,5,6-dibenzofluorenone (VI), 1,2,7,8-dibenzofluorenone (VII) and 1,2,3,4-dibenzofluorenone (VIII). For (VI) and (VII), this effect can also be predicted by the method of molecular orbitals<sup>15</sup>. It is interesting to compare with fluorenone (IV), xanthone (IX) which is well known to retain some of the character of its parent substance  $\gamma$ -pyrone (as Ia)<sup>8</sup>. (IX) has indeed a very "polar" carbonyl frequency.

In connection with a theoretical study of the influence of methyl groups on the fine structure of benzofulvenes and dibenzofulvenes<sup>16</sup>, 2-methyl-fluorenone, 3-methyl-fluorenone and

\* Received May 1951



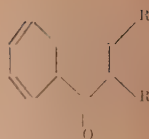
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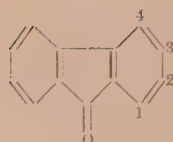
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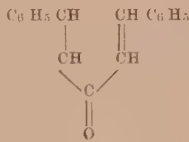
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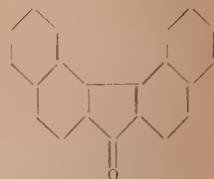
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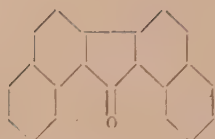
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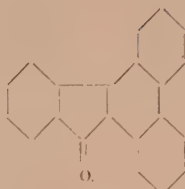
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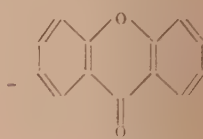
VI



VII



VIII



IX

2,3-dimethyl-indone (III,  $R=CH_3$ ) were investigated. They are more polar than fluorenone and 2,3-diphenylindone, although they do not reach the values characteristic for benzophenone or (V).

TABLE I. Carbonyl Frequency ( $cm^{-1}$ )  
of Ketones

Acetone	1718
Benzophenone	1663
Dibenzylidene-acetone (V)	1656
Tetraphenyl-cyclopentadienone (II)	1710
2,3-Diphenylindone (III, $R=C_6H_5$ )	1710
Fluorenone (IV)	1718
3,4,5,6-Dibenzofluorenone (VI)	1684
1,2,7,8-Dibenzofluorenone (VII)	1694
1,2,3,4-Dibenzofluorenone (VIII)	1697
Xanthone (IX)	1638
2-Methyl-fluorenone	1690
3-Methyl-fluorenone	1684
2,3-Dimethylindone (III, $R=CH_3$ )	1684

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# A NEW SYNTHESIS OF FATTY ACIDS \*

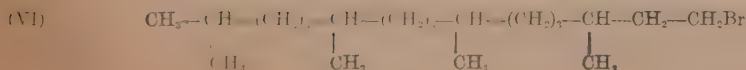
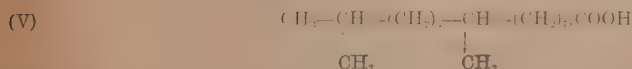
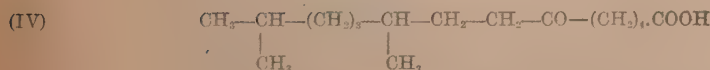
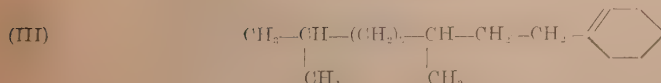
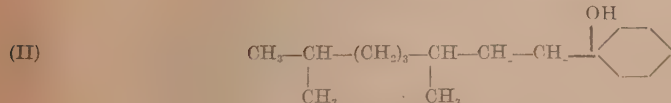
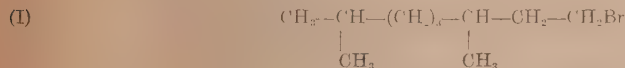
The discovery of branched and, therefore, optically active fatty acids in nature - e.g. of tuberculostearic acid ( $C_{18}H_{37}COOH$ ) and phthioic acid ( $C_{22}H_{41}COOH$ ) in tubercle bacilli<sup>1,2</sup> - has led to the development of new methods applicable to the synthesis of these unusual types of molecules. The following method appears to have the advantage of being comparatively simple and adaptable to the use of naturally occurring (or synthetically imitated) optically active starting materials of known configuration.

Tetrahydrogeranyl bromide (I), easily accessible from geraniol<sup>3</sup> was converted into its magnesium derivative and the latter condensed

with cyclohexanone to give tetrahydrogeranyl-cyclohexanol (II), b.p.  $110-112^\circ$  (0.02 mm). (*Anal.* Calcd. for  $C_{16}H_{32}O$ : C, 79.9; H, 13.4. Found: C, 80.0; H, 13.6). Dehydration by means of potassium bisulfate at  $160^\circ$  led to tetrahydrogeranylcyclohexene (III), b.p.  $104^\circ$  (0.02 mm). (*Anal.* Calcd. for  $C_{16}H_{30}$ : C, 86.4; H, 13.6. Found: C, 86.5; H, 13.4). This could be ozonised in ethyl bromide solution<sup>4</sup> to 6-keto-9,13-dimethyl-tetradecanoic acid (IV). Distillation of this material (viscous yellow oil) could not be accomplished at 0.01 mm due to decomposition. (*Anal.* Calcd. for  $C_{16}H_{30}O_2$ : C, 71.1; H, 11.2. Found: C, 71.3; H, 11.4). The ethyl ester of (IV) was also prepared by the method of Cason<sup>5</sup> from (I), magnesium, cadmium chloride and ethyl adipoyl chloride. Saponification gave (IV) as shown by the analysis of the product.

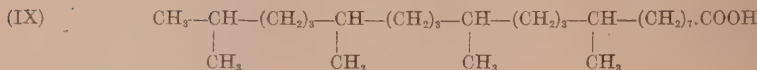
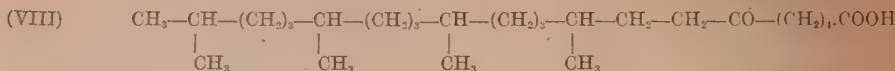
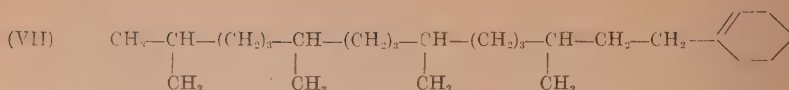
(IV) was reduced by the method of Huang-Minlon<sup>6</sup> to 9,13-dimethyl-tetradecanoic acid (V), b.p.  $135-136^\circ$  (0.01 mm), a pale yellow oil. The hydrazone formation required a reflux time of at least two hours. Heating for shorter periods of time led to incomplete hydrazone formation and therefore incomplete reduction. (*Anal.* Calcd. for  $C_{16}H_{32}O_2$ : C, 75.0; H, 12.6. Found: 75.3; H, 12.4).

(V) was characterised by a well crystallised p-bromo-anilide, m.p.  $70-71^\circ$  (needles from aqueous methanol). (*Anal.* Calcd. for  $C_{22}H_{36}OBrN$ : C, 64.4; H, 8.8. Found: C, 64.5; H, 8.9).



\* Received May 1951.





Analogously, the Grignard derivative of  $\alpha$ -hydrophytyl bromide (VI)<sup>7</sup> gave with cyclohexanone dihydrophytyl-cyclohexanol, b.p. 140-150° (0.1 mm). (Anal. Calcd. for  $\text{C}_{26}\text{H}_{50}\text{O}$ : C, 82.0; H, 12.8. Found: C, 81.7; H, 12.6). This alcohol could be dehydrated to dihydrophytyl-cyclohexene (VII) at 180° by means of p-toluene-sulphonic-acid.

No further work was done on the ozonisation of VII.

The ethyl ester of (VIII) was prepared from (VI), magnesium, cadmium chloride and ethyl adipoyl chloride.

The keto acid (VIII) was prepared by saponification of the ester and was obtained in the form of a yellow oil (Anal. Calcd. for  $\text{C}_{26}\text{H}_{50}\text{O}_3$ : C, 76.0; H, 12.3. Found: C, 76.4; H, 12.6.) which was reduced by the Huang-Minlon method, as before, to 9,12,16,21-tetramethyl-docosanoic acid (IX), b.p. 177-179° (0.001 mm). (Anal. Calcd. for  $\text{C}_{26}\text{H}_{52}\text{O}_2$ : C, 78.7; H, 13.2. Found: C, 78.8; H, 13.3).

(IX) is isomeric with phthioic acid.

The potentialities of the synthetic method which involves ozonisation are obvious. It permits the lengthening of any chain available in the form of a bromide capable of giving a magnesium derivative, by a straight chain of six carbon atoms where the terminal one is a carboxyl group. The use of substituted cyclohexanones permits the introduction of further branches of the main carbon chain. The method is further adaptable to cyclopentanone and cycloheptanone. Finally, it should be borne in mind that the reduction of the carboxyl group to a primary alcohol, which is easily carried out by means of lithium aluminium hydride, leads to substances with which a further number of transformations can be performed.

This investigation was carried out at the Chemical Laboratories of Harvard University, with the kind permission of Prof. L. F. Fieser.

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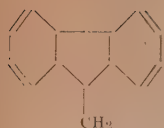
#### ABNORMAL SUBSTITUTION REACTIONS IN THE 3,4,5,6-DIBENZOFULUORENE SERIES\*

The calculation of the properties of the benzo-derivatives of dibenzofulvenes (I) by the method of the molecular orbitals<sup>1</sup> has led to the picture (II) for the 3,4,5,6-dibenzo-derivative of (I), in which the figures represent the electric charges (in fractions of one electron) concentrated at each carbon atom. In comparison with the corresponding picture (Ia) of (I), the reduction in polarity of the semicyclic double bond and the increased negative charges at C<sub>2</sub> and C<sub>7</sub> are remarkable.

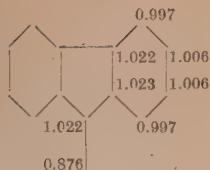
This picture may explain two abnormal observations which are reported here.

1. While fluorene and most of its nuclear substitution products are brominated in the 9-position by N-bromosuccinimide<sup>2</sup>, 3,4,5,6-di-

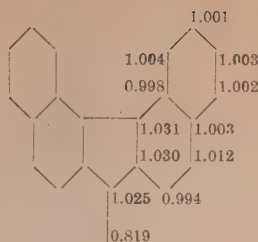
\* Received May 1951



I



Ia



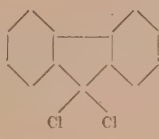
II



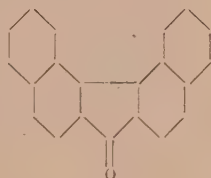
III



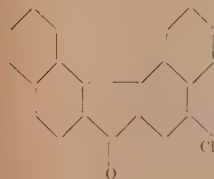
IV



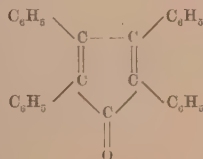
V



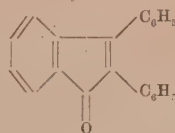
VI



VII



VIII



IX

benzofluorene (III)<sup>4</sup> gives a nuclear monobromo-derivative. It crystallises from a mixture of benzene and petroleum ether and has m.p. 169.5–171°. (*Anal.* Calcd. for  $C_{21}H_{13}Br$ : C, 73.0; H, 3.8; Br, 23.2. Found: C, 72.7; H, 3.8; Br, 23.2). The bromine atom is not attacked by alkali and therefore cannot occupy the 9-position<sup>5</sup>. This was confirmed by the oxidation of the substance which led to a brominated 3,4,5,6-dibenzofluorenone, red prisms from benzene, m.p. 218–219.5°. (*Anal.* Calcd. for  $C_{21}H_{11}OBr$ : C, 70.2; H, 3.1; Br, 22.3. Found: C, 70.4; H, 3.3; Br, 22.6). In view of the general behaviour of the fluorene system<sup>6</sup>, it is assumed that the bromine atom enters (III) in the 2-position (IV).

Substitution of aromatic hydrogen by N-bromosuccinimide is fairly infrequent<sup>7</sup>.

2. While fluorenone reacts with phosphorus pentachloride to give 9,9-dichlorofluorene (V)<sup>8</sup>, 3,4,5,6-dibenzofluorenone (VI)<sup>8</sup>, when heated at 160° with this reagent, preserves its carbonyl group. Instead, a monochloro-derivative of (VI) is formed, for which the tentative formula (VII)

is suggested. (VII) forms red needles of m.p. 200–201° (from acetic acid) (*Anal.* Calcd. for  $C_{21}H_{11}OC1$ : C, 80.3; H, 3.5; Cl, 11.1. Found: C, 80.0; H, 3.5; Cl, 11.1). This behaviour recalls the observation<sup>9,10,11</sup>, that tetraphenylcyclopentadienone (VIII) and 2,3-diphenylindone (IX) upon treatment with phosphorus pentachloride, react at their C=C double bonds, giving dichloro-addition products (and phosphorus trichloride).

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#### THE OCCURRENCE OF d-CAMPHOR IN AN ISRAELI ARTEMISIA SPECIES\*

The leaves of *Artemisia arborescens*, which abounds in the northern part of Israel, contains an essential oil (0.72%), characterised by a high azulene content. Distillation under 20 mm pressure gave a series of intensely blue fractions (from 123–158°C) from which a mixture of two azulenes was isolated in the usual manner, by extraction of their solution in pentane with concentrated aqueous phosphoric acid<sup>1</sup>. The two azulenes which have not yet been finally identified, have the composition  $C_{15}H_{18}$  and are characterised by trinitrobenzene derivatives of m.p. 115 and 134°, respectively. The absorption spectrum of the mixture is reproduced in Fig. 1.

Of the two colourless head fractions (70–90° and 90–115°), the second one was observed to crystallise almost completely. The solid product was purified by sublimation and identified as

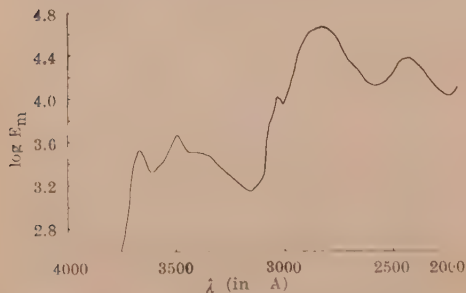


Figure 1

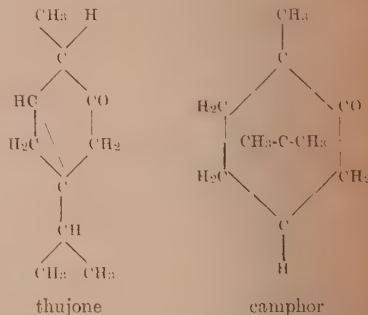
Spectrum of the alcoholic solution of the azulene from *Artemisia arborescens*

\* Received May 1951.

camphor by its odour, melting point (178°) and mixed melting point with an authentic specimen.  $[\alpha]_D^{20} = +41.0^\circ$  (in alcohol,  $c = 10\%$ ).

The camphor content of the oil was 13.8% that of the leaves, therefore, 1%.

Camphor has been observed before<sup>2</sup> in *Artemisia* species, but not in *A. arborescens*. In the cases reported in the literature, however, laevorotatory camphor was found [e.g. *A. Herba-alba*, *A. maritima* var. *astrachanica* (90.87% l-camphor)], *A. cana*, *A. caspia* var. *citriodora*, *A. tridentata*], and also borneol (e.g. *A. frigida*, *A. annua*, *A. maritima* var. *Kazakewicz*). From the biogenetic point of view, it is interesting to note that in other varieties of *A. arborescens* (and in some other *Artemisia* species) thujone has been discovered, which is an isomeride of camphor.



The author wishes to express her appreciation of the contribution made by Moshe Zwick to this investigation.

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#### RESPONSE OF *p*-AMINO BENZOIC ACID REQUIRING ORGANISMS TO *p*-AMINOPHENYLALANINE\*

Ch. Weizmann<sup>1</sup> has observed that *p*-aminophenylalanine (PAPA) acts as growth factor for *Cl. acetobutylicum* and is about 10 times as active as the "normal" growth factor *p*-aminobenzoic acid (PABA). This is particular-

\* Received May 1951.

ly noteworthy as other, similar substances have only an extremely limited growth-promoting activity, e.g. *p*-aminophenylacetic acid<sup>2</sup>, to which PAPA could be related biologically.

The response to PAPA of other PABA-requiring microorganisms seemed therefore worthy of study. A *p*-aminobenzoic acid-requiring mutant of *E. coli* (ATCC 9723 a)<sup>3</sup> which gives full growth at 37°C in 18 hours with 0.01  $\gamma$ /ml of PABA, responded positively to small quantities of PAPA; maximum response was reached at 1  $\gamma$ /ml (Fig. 1). In large doses, PAPA

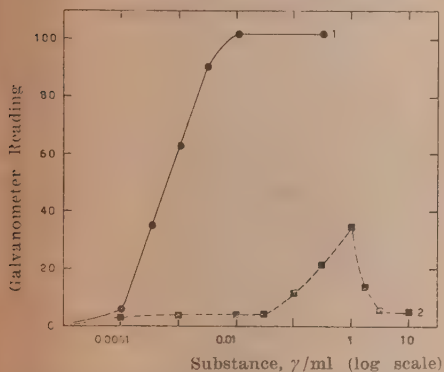


Fig. 1. — Growth response of the PABA-requiring *E. coli* mutant to PABA (Curve 1) and PAPA (Curve 2).

showed an inhibiting effect, probably due to the antagonism with phenylalanine<sup>4,5</sup> which was marked at these levels of PAPA. Therefore, it might have been expected that addition of phenylalanine would relieve this inhibition and thus increase the utilisation of PAPA. However, Fig. 2 shows that phenylalanine somewhat suppresses the utilisation of PAPA. At

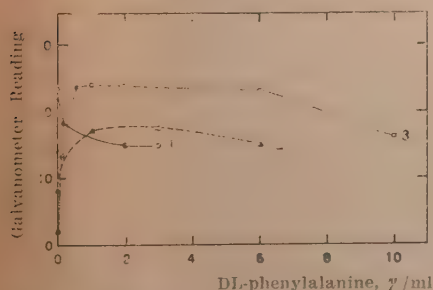


Fig. 2. Effect of DL-phenylalanine on utilisation of PAPA by PABA-requiring *E. coli* mutant. Curve 1, 2 and 3: growth in the presence of phenylalanine and 1.0, 2.5 and 5.0  $\gamma$ /ml PAPA, respectively.

levels of the latter, higher than 1  $\gamma$ /ml, the growth response in the presence of phenylalanine is almost the same as for 1  $\gamma$ /ml of PAPA alone (and not higher as was expected).

As to the effect of PAPA on the utilisation of PABA, it was observed that quantities of PAPA larger than 1  $\gamma$ /ml inhibit this utilisation; up to that level, its effect is additive to that of PABA (Fig. 3).

The inhibition of *E. coli* wild type (ATCC 9723) by sulfanilamide is relieved by *p*-amino-

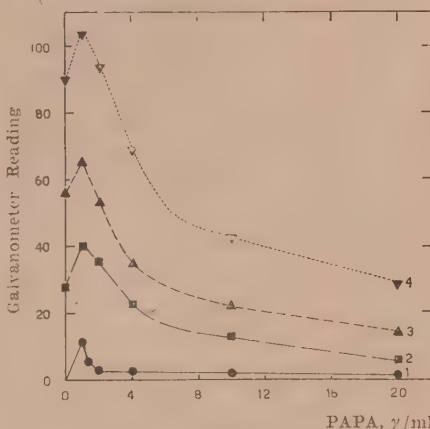


Fig. 3. — Growth response of PABA-requiring *E. coli* mutant to PABA in presence of PAPA. Curve 1: PAPA alone. Curve 2, 3 and 4: PAPA and 0.0005, 0.001 and 0.005  $\gamma$ /ml PABA, respectively.

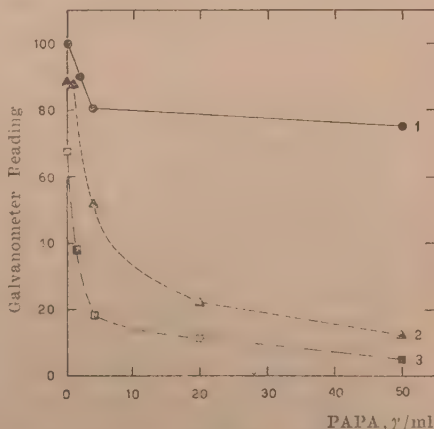


Fig. 4. — Effect of sulfanilamide and PAPA on growth of *E. coli*, wild type. Curve 1: PAPA alone. Curve 2 and 3: PAPA in presence of 45 and 60  $\gamma$ /ml. sulfanilamide, respectively.



benzoic acid, *p*-Aminophenylalanine cannot replace PABA; on the contrary, it is a synergist of sulfanilamide (Fig. 4). If both PAPA and sulfanilamide are added to a culture of *E. coli*, PABA reverses the sulfa-inhibition, yielding a growth corresponding to that found in presence of PAPA alone, and phenylalanine reverses the action of PAPA, yielding a growth corresponding to that found in presence of the sulfa-drug alone. The PAPA-sulfa inhibition is overcome by PABA and phenylalanine together.

It has been found previously<sup>4</sup> that PAPA inhibits the growth of *E. coli*, wild type and its phenylalanineless and tyrosineless mutants,<sup>5</sup> and that this inhibition is relieved by phenylalanine, tyrosine or tryptophane. It has further been shown<sup>5</sup> that in certain concentrations, it stimulates the growth of the tyrosineless mutant. The observation that PAPA can partially replace *p*-aminobenzoic acid, adds a further facet to the picture of this "multiple effect" biological agent.

Parallel experiments were carried out with *Acetobacter suboxydans* (ATCC 621)<sup>6</sup> and *Lactobacillus arabinosus* (17-5)<sup>7</sup>. With the former organism, the quantity ratio between PABA (0.0027.  $\gamma$ /ml) and PAPA (20  $\gamma$ /ml), yielding 76% of full growth, was 1:7,400; increase of PAPA up to 100  $\gamma$ /ml did not increase the growth. For the latter organism, the PABA: PAPA ratio (0.0004 and 15  $\gamma$ /ml, respectively) yielding full growth was 1:37,500.

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#### INTENSITIES OF THE ULTRAVIOLET ABSORPTION BANDS OF THE FULVENES\*

Investigation of the absorption spectra of the fulvenes, benzofulvenes and dibenzofulvenes (I, II, III)<sup>1</sup> has confirmed the calculations made by means of the method of molecular orbitals<sup>2,3</sup>. This agreement was confined so far to the wave-lengths of the bands observed. The theoretical intensities of the absorption have now been calculated and compared with the experimental values; the calculations refer to the transition  $N \rightarrow V_1$ , i.e. the absorption band of longest wave-length. The mean oscillatory force of an electronic transition is linked to the observed molecular extinction coefficient  $\epsilon_r$  ( $r$  in cm<sup>-1</sup>) over an appreciably large range of frequencies, by the following equation:

$$(1) \quad f_{\text{exp.}} = 4.32 \cdot 10^{-9} \int \epsilon_r \, d\nu$$

Theoretically,  $f$  [the probability of the transition from the ground state ( $\psi_g$ ) to an excited state ( $\psi_m$ )] is given by

$$(2) \quad f_{\text{theor.}} = 1.085 \cdot 10^{11} \, \nu \bar{D}, \text{ where } D, \text{ the dipolar force is}$$

$$(3) \quad D = GQ^2 \quad (G=1 \text{ for transitions between non-degenerate states}). Q, \text{ the transition moment, is given by (4):}$$

$$(4) \quad Q = \int \psi_g^* \sum_r \vec{e}_r \psi_m \, d\tau$$

$\vec{e}_r$  being the vector, defining the position of the atom in the molecule<sup>4</sup>. It is known that for benzene and ethylene derivatives,  $f_{\text{theor.}}$  and  $f_{\text{exp.}}$  differ by a factor of 0.3-0.4.

In Table I,  $f_{\text{theor.}}$  and  $f_{\text{exp.}}$  are listed for a series of fulvene derivatives. In view of the instability of the fulvenes (I, II, III), the  $f_{\text{exp.}}$  have been determined for methyl-isobutyl-fulvene<sup>5</sup>, isopropylidene-indene<sup>6</sup> and ethylidene-fluorene<sup>6</sup>, respectively; it can be assumed that apart from hyperconjugation effects, the alkyl-substitution will not significantly alter the spectra of the parent substances.

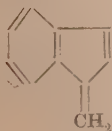
\* Received May 1951.

TABLE I  
Intensities of Absorption Bands of the Fulvenes

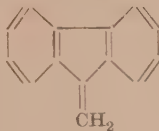
Substance	Q (A)	D (A) <sup>2</sup>	Transition Energy (in $\gamma$ )	$\nu_{\text{obs.}}$ (cm <sup>-1</sup> )	$f_{\text{theor.}}$	$f_{\text{exp.}}$	$\frac{f_{\text{exp.}}}{f_{\text{theor.}}}$	Polarisation, relative to semicyclic double bond
Fulvene (I)	0.47	0.22	0.807	27,000	0.064	0.012	0.19	perpendicular
Benzofulvene (II)	1.54	2.36	0.882	31,400	0.800	0.433	0.54	angle of 30°
Dibenzofulvene (III)	1.68	2.81	1.033	35,500	1.082	0.464	0.43	parallel
Dibiphenylene-ethylene (IV)	1.37	1.87	0.621	21,700	0.442	0.334	0.76	parallel
Dibiphenylene-butadiene (V)	3.91	10.27	0.515	23,400	2.61	0.790	0.33	parallel



I



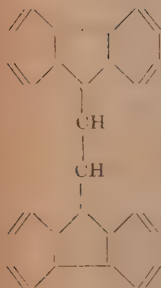
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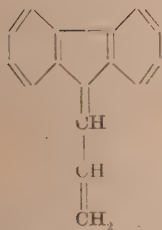
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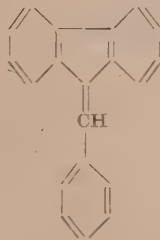
IV



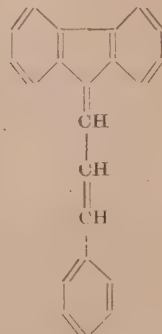
V



VI



VII



VIII

In agreement with the theory, the intensity increases from (I) to (III); the sequence is, therefore, reverse to that obtained in the series naphthalene, anthracene, naphthacene<sup>6</sup>. Similarly, one can calculate for biphenylene-butadiene (VI) the probable wave-length  $\nu$  and  $f_{\text{theor.}}$  as 25,800 cm<sup>-1</sup> and 2.145 [if  $\gamma_{\text{spect.}}$  is assumed to be 34,000 cm<sup>-1</sup> (as in the simple fulvenes) or as 30,400 cm<sup>-1</sup> and 2.530 [if the higher value of 40,000 cm<sup>-1</sup> is adopted, taking into account that the extension of the conjugation would cause  $\gamma_{\text{spect.}}$  to be higher (cf. (V):  $\gamma_{\text{spect.}}$  = 45,000 cm<sup>-1</sup>)]. In any event, the intensity of the longest absorption band is

bound to be higher than for (III). That this conclusion is justified, can be seen (as (VI) is unknown) from a comparison of benzyldiene-fluorene (VII,  $\nu$  = 30,700 cm<sup>-1</sup>,  $f_{\text{exp.}}$  = 0.524) and cinnamylidene-fluorene (VIII,  $\nu$  = 25,700 cm<sup>-1</sup>,  $f_{\text{exp.}}$  = 0.903) which are related to each other in the same way as (VI) and (III).

It is surprising that dibiphenylene-ethylene (IV) deviates so much from the other compounds studied regarding the correction factor ( $f_{\text{exp.}}$  :  $f_{\text{theor.}}$ ). Following previous investigations<sup>1,2,3</sup>, one will ascribe this effect to the non-planarity of this molecule. A planar

form of (IV) would probably absorb at a shorter wave-length. Indeed, if one adopts for  $\gamma$  spect. the value of 45,000  $\text{cm}^{-1}$  from (V),  $\nu$  would be 28,000, instead of 21,700  $\text{cm}^{-1}$ , and  $f_{\text{theor.}} = 0.568$ .

This would bring the correction factor down to the more fitting value of 0.59. Occasionally, the suggestion has been made that (IV) represents a free biradical. However, calculation shows that a free fluorenyl radical should absorb approximately at 14,500  $\text{cm}^{-1}$  and that the intensity of this absorption band should be very low ( $f_{\text{theor.}} = 0.043$ ). Obviously a radical formula for (IV) would not be justified.

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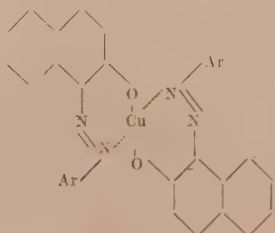
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#### COPPER COMPLEXES OF SUBSTITUTED 1-BENZENEAZO-2-NAPHTHOLS

o-Hydroxy-azo dyes give complex metal, e.g. copper derivatives, which probably have to be formulated as follows:



The ability of the nitrogen atoms to participate in the formation of the complex, will be influenced by substituents in the Ar nucleus, but no systematic work appears to have been done in this direction.

When equivalent quantities of 1-(benzene-azo)-2-naphthol and copper tetrammine sulphate are heated in form of an intimate mixture<sup>1</sup>, the dark copper complex begins to form at 200°, and ammonia is liberated. Under the same conditions, 1-(4'-nitrobenzene-azo)-2-naphthol reacts at 100°, and 1-(2',4'-dinitrobenzene-azo)-2-naphthol at 60°.

The complexes can be isolated in practically pure form, when the reaction products are treated with water, alcohol, ether, acetone and pyridine. They are dark-brown insoluble powders. For the nitrobenzene-azo-derivative, a copper content of 9.5% was found (Calc.: Cu, 9.8), for the dinitrobenzene-azo-derivative, a copper content of 7.7% (Calc.: Cu, 8.7).

The activation of the azo-nitrogen by the nitro-groups in *ortho*- and *para*-position obviously parallels the increase of the electrolytic dissociation constant from phenol through 4-nitrophenol to 2,4-dinitrophenol (1:500:10<sup>6</sup>) and its decrease from aniline to 4-nitroaniline (4000 times).

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1. See British Patent 371, 188 (1932).

#### REPRODUCTIVE BEHAVIOUR OF THE LEVANTE VOLE (*Microtus guentheri* D. A.)

Reproductive behaviour begins with mating, and continues until weaning of the young, or to end of care of young if it continues after weaning.

Mating was observed to occur at any stage of the estrous cycle, but mainly during estrus and pro-estrus (anestrus—no matings in three cases; pro-estrus—15 matings in 26 cases; estrus—16 matings in 29 cases; metestrus—four matings in 70 cases; diestrus—one mating in 13 cases). The difference was found highly significant statistically.

The mating period was always divided into several groups of a number of copulations each. The intervals between the groups grew successively longer, probably due to exhaustion of the male.

The time interval from pairing until first copulation was nil in seven cases, up to ten minutes in 27 cases and over 20 minutes in five cases. The number of copulations per mating period of two hours was 1-10 in six cases, 11-20 in 13 cases, 21-30 in 11 cases, 31-40 in four cases, 41-50 in three cases, over 51 in four cases, with a maximum of 101 copulations per mating period (two hrs.).

Previous sexual experience has definite bearing on the mating behaviour. In experiments where the vaginal smear of the female partner showed estrus or pro-estrus, the greatest occurrence of matings was in the case where both partners were experienced (18 out of 20); male only experienced—five out of 11; female only experienced—five out of 12; both virgin 2 out of 10. These figures are for two-hour-mating-periods. The differences have been proven to be significant statistically (as have all figures given in this work).

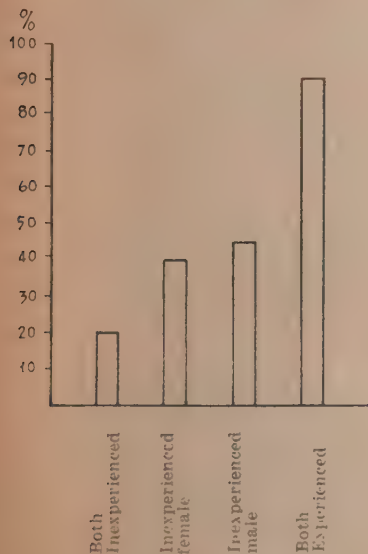


Figure 1

Previous sexual experience as a factor in mating behaviour (estrus and pro-estrus)

Nest building was observed in all types of adult voles, and in all seasons of the year. The nests were either tunnel-shaped, or open like a bird's nest. Of 458 cages observed 29 showed no nest at all (18%), 44 were tunnel-type (28%), and 85 were 'bird's-nest' type (54%). Young laboratory-born individuals tended to build the tunnel-type.

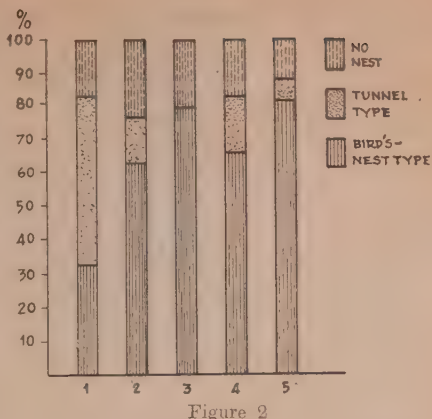


Figure 2

Nest-types in different groups of individuals

- Group 1: Young laboratory-born individuals
- Group 2: Young field-born females
- Group 3: Laboratory-born pairs which never had young
- Group 4: Field-born pairs, no young
- Group 5: Laboratory-born pairs, had young

Both parents were observed to share equally in care of the young. The male takes equal part in all tasks, and is even more willing than the female to adopt young from other parents. 110 out of 178 females accepted strange young, 81 males out of 111 accepted such young. The difference is much more striking when considering only individuals with no previous maternal experience. In this group five females out of 34 accepted the young proffered, while 17 out of 33 males accepted them. The same, if to a lesser extent, is true of the group with previous births but no young at the time of the experiment; the male-female ratio is almost equal with animals having young at time of experiment. The voles with young receive more easily such young as approach their own in age, though age proved no factor in acceptance by voles without young at the time of the experiment.

Natural weaning occurs at 18 to 20 days. The earliest forced weaning obtained in our experiments was 9 days (10 grams in weight), and 12 days (6.3 grams), provided an adult (male or non-nursing female) were present to care for them.

In prolonged-maternity experiments, done by exchanging young each day from own mother to experimental animal, two such experimental animals continued their maternal behaviour for 249 and 317 days respectively, and would have continued but for the lack of appropriate young. Milk supply ceased after 34 and 25 days respectively.



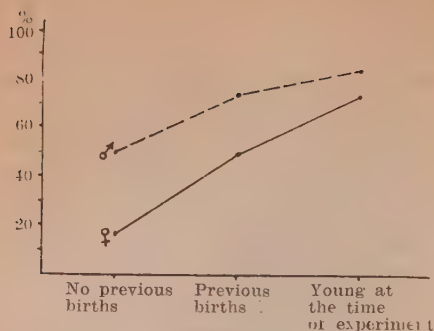


Figure 3

Acceptance of strange young by adult *Microtus*

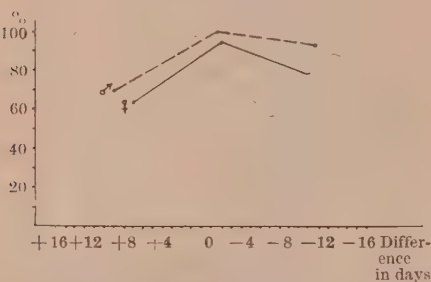


Figure 4

Acceptance of strange young by adults with young, considering difference in age between strange young and own young

#### Discussion of literature:

For the biology of the Levante vole see Bodenheimer<sup>1</sup>.

Mating: Reed and Reed<sup>2</sup> report a similar mating-pattern, for the golden hamster, to that described by us. They claim it takes 14–40 copulations before semen ejection can be effected; there are 5–8 ejaculations per mating period. Griffith and Farris<sup>3</sup> tell of 15–70 copulations per mating-period in the white rat. Allan<sup>4</sup> and Reed and Reed<sup>2</sup> both mention lengthening of the successive intervals between groups of copulations.

Munn<sup>5</sup>, states that mating in the white rat may occur at any point during the estrous cycle, though estrus (greatest confirmation) is the usual time. Other writers give estrus as the only time of copulation.

Nest-building: Wiesner and Sheard<sup>6</sup> state for the rat that nest-building reaches its climax just before parturition, and declines within 10–20 days. We have not found this true for voles.

Care of young: Hatfield<sup>7</sup> reports that in captivity, the male of *Microtus californicus* participates in care of the young, "contrary to the natural state".

Acceptance of strange young: Wiesner and

Sheard<sup>6</sup> state for the rat that only such individuals as have young at that time, accept strange young. We did not find it so for our voles. Wiesner and Sheard<sup>6</sup> also state that the age of the young proffered is a factor in acceptance, and we agree with them for our corresponding group of adults with young.

Prolonged maternity: We patterned our experiment after that of Wiesner and Sheard<sup>6</sup>, who had succeeded in prolonging maternal behaviour to 13 months in one case.

This work was done at the *Microtus* laboratory of Professor F. S. Bodenheimer, from April 1949 to September 1950. The part on the estrous cycle of the female was done with the help of Dr. W. Lash of the same laboratory.

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#### A NEW OCCURRENCE OF MARINE TRIASSIC IN ISRAEL

The existence of marine Triassic in Israel first became known some ten years ago through the work of the geologists of the Iraq Petroleum Co. They discovered beds of Triassic age in the Makhtesh (erosion cirque) of Wadi Raman. The results of their work were published in part by Shaw<sup>1</sup>. During the geological mapping of the Negev on the scale of 1:100,000, begun by the authors more than two years ago and now completed, a new occurrence of marine Triassic was encountered this time in the dome of Har Arif (Jebel Ureif), a distance of 20 km southwest of Wadi Raman. In the centre of this dome there occur two "Makhteshim". The western-most is stratigraphically the deeper one. Underlying the Nubian Sandstone, there is a series of dark, partly dolomitic limestones alternating with thin horizons of greenish marls. Some trachytic dikes pierce this series, which constitutes the oldest beds outcropping

in that area. The series is exposed to a depth of 9 metres only and is cut off on its northern side by the Arif-fault. The length of the outcrop does not exceed 100 metres. Some of the beds are very rich in fossils, among which the following have been recognized: *Encrinurus liliiformis*, *Gervillia* sp., *Myophoria* sp. and a *Ceratites* sp., a smooth type with a sharp dorsal carina and an obtuse carina on the sides. In lithology as well as in their fossil contents, these beds are very similar to those of the Limestone-Dolomite-Marl Series of the Triassic in Wadi Raman<sup>2</sup>, which belongs to the Muschelkalk. There can be no doubt, that these beds of Har Arif belong to the same age. It should be noted, however, that the fossiliferous strata of Wadi Raman occur mainly at the base of the series which there attains a thickness of 170 metres.

The marine transgression of the Triassic therefore penetrated at least as far south as Har Arif. In the Menaiye area, however, (no strata older than the Lower Cretaceous are exposed between these points) the Triassic section is already developed in the Nubian Sandstone facies and is therefore probably terrestrial.

Although the Muschelkalk-Series of Wadi Raman and Har Arif are developed in a very similar manner, the overlaying strata are entirely different in these two places. In Wadi Raman there follows on top of the Muschelkalk a lagoonal gypsum series, 175 metres thick and very probably belonging to the Keuper. This series is overlain in turn by partly marine, partly terrestrial beds of Jurassic age, totalling almost 500 metres. In Har Arif, however, the thick gypsum series is entirely lacking. There follows, overlying the Muschelkalk, a series, 30 metres thick, of well-bedded marine sandstones markedly conglomeratic at their base, which could be the littoral equivalent of the lagoonal Keuper of Wadi Raman but may already belong to the Jurassic.

As to the tectonic position of this Triassic outcrop of Har Arif, a very remarkable peculiarity should be mentioned. The Triassic section is separated from the rocks of the Cenomanian transgression by not more than 50 metres of strata, mainly sandstones and basalts. Immediately outside the core of the structure, 1 km further west, at least 250 metres of post-Triassic rocks, underlying the Cenomanian, are visible. In the core of the Arif-dome the thickness of these strata is therefore drastically reduced. A similar phenomenon appears in Wadi Raman. Not only does the Lower Marine Series of the Jurassic (Dogger?) rest there with angular unconformity on the Triassic, but again in the core of the structure the Upper Triassic and Jurassic sediments are markedly reduced in thickness. The absence of some formations and the small development of

others in the core of both structures and there alone points strongly to the existence of a folding-phase of post-Muschelkalk and pre-Cenomanian age. The best evidence so far available for the age of these tectonic movements points to Upper Triassic and/or Lower Jurassic time. The sudden onset of magmatic activity during the Jurassic, the first since pre-Cambrian time, fits well into this picture. It has become clear during the last years that the tectonic history of the mountain ranges in the central Negev can be traced back to Turonian time<sup>3</sup>. It now seems possible that it should be pushed further back even into the Lower Mesozoic.

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#### IMMUNOLOGICAL OBSERVATIONS ON *TRYPANOSOMA LEWISI*\*

The immunology of *Trypanosoma lewisi* infections in the rat has been investigated by a number of observers since 1898 when Kantback Durham and Blandford<sup>1</sup> first demonstrated that animals which have recovered from an infection are immune to further attacks. Rabinowitsch and Kempner<sup>2</sup> first demonstrated the prophylactic action of the serum of rats recovered from artificial infections. Novy, Perkins and Chambers<sup>3</sup> demonstrated that injections of cultures of *T. lewisi* which have lost their infectivity for rats render these animals immune to infective strains. Taliaferro<sup>4,5,6</sup> carried out extensive investigations on the serology of *T. lewisi* infections in rats.

Novy, Perkins and Chambers<sup>3</sup> concluded that the serum of rats immunized by non-infective cultures has no prophylactic value. Gruner<sup>7</sup> demonstrated clearly that the serum of rats immunized by non-infective cultures has no prophylactic action immediately after the establishment of immunity or subsequently.

\* Received December 10, 1951.

Using a strain of *T. lewisi* (isolated in 1939 in the Department of Parasitology of the Hebrew University, Jerusalem) which had become non-infective in the course of continuous passage in cultures, we were able to confirm the above finding.

In addition, the following facts were established:

1. The serum of animals with a solid immunity produced by injections of a non-infective strain never shows prophylaxis against an infective strain of *T. lewisi* (20 rats). On the other hand, immune serum produced by injecting rabbits with the same non-infective strain has a prophylactic action on rats. As little as 0.1 cc. administered 10 minutes after the inoculation of an infective strain gave complete protection. Moreover, the immune rabbit serum prepared from non-infective cultures has an immediate agglutinating and lytic action on infective strains of *T. lewisi*. (Serum of rats immunized by non-infective cultures has neither agglutinating nor lytic action on infective strains. On the other hand, serum of rats recovered from infection agglutinates infective trypanosomes. Augustine<sup>8</sup> considers the agglutinins to be a factor in the immunity of recovered animals).

2. The serum of rats recovered from an infection of *T. lewisi* has a prophylactic action during the first month or so after recovery from infection. Subsequently the serum of these animals loses demonstrable prophylactic action in spite of the persistence of a solid immunity. At this stage their serum resembles that of animals with a solid immunity produced by non-infective cultures. It therefore seems that a solid immunity persists both in the case of animals after recovery from experimental infection as well as in the case of animals immunized by non-infective cultures, in the absence of demonstrable serological findings, i.e. prophylactic action, lysis and agglutination.

I wish to thank Professor S. Adler for his advice and guidance.

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#### THE LIFE CYCLE OF *BRACHYCAUDUS AMYGDALINUS* SCHOUT. (APHIDIDAE, HOMOP.) IN ISRAEL

*Brachycaudus amygdalinus* is a serious pest to almond trees in Israel, sitting on the leaf's lower side and causing its curling. The life cycle of this aphid was not known and only parthenogenetic forms were described. Bodenheimer<sup>1</sup> mentions this aphid in the copresence of the list of Aphids, and Plaut<sup>2</sup> has found its colonies on almond trees from February till June.

Hille Ris Lambers' suspicion that the summer host of this aphid is *Polygonum* was confirmed and so *Brachycaudus abnormis* H.R.L. and *B. amygdalinus* Schout. are synonymous. On *Polygonum*, the aphids reproduce parthenogenetically throughout the year and the population peak is reached in spring. Gynoparae and males leave *Polygonum* in autumn and migrate to almond trees. The gynoparae produce sexual females, which lay eggs in the crevices of the bark and in the axils of buds. In the coastal plain the eggs hatch in February and by spring, a large population has been built up on almond trees. Alate forms appear during the later half of spring and migrate to *Polygonum*. After almost all the alates have left the almond trees, there remain the apterae and nymphs which disappear in June. The dispersal of aphids from tree to tree during spring is very small, because the alates are not the responsible agent.

Population fluctuations are greatly determined by the climatic conditions during the infestation period of the almond trees and in the spring, by the age of the leaves and their physiological condition, and by the agrotechnical routine. The varieties Non-Pareil and Ne-Plus-Ultra; in contrast to Victoria and Greek, are only slightly infested in the coastal plain where irrigation is practised. These varieties are unsatisfactory hosts because they annually lose their leaves in the autumn and blossom late in the spring. Predators and parasites destroy considerable quantities of aphids, but they are not the chief factors in lowering the population peak.

Conditions in Israel may induce the formation of sexuals, which infest the almond trees. However, conditions necessary for the obligatory suppression of a parthenogenetic cycle during the



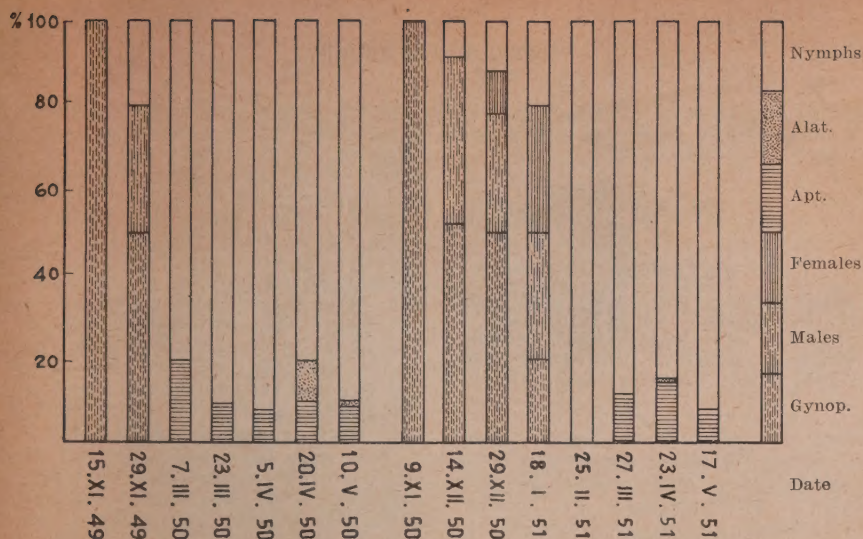


Fig. 1. Structure of *Brachycaudus amygdalinus* Schout. on almond trees at Mikve-Israel, during the period: November 1949–May 1951

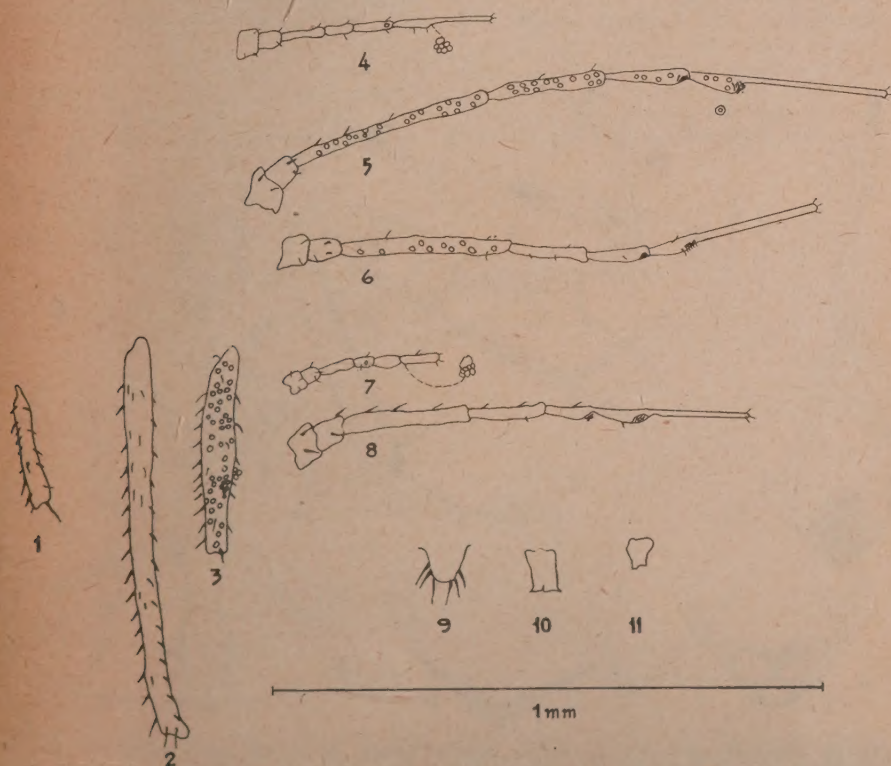


Fig. 2. *Brachycaudus amygdalinus* Schout.

1-3. HIND TIBIA 1) apterous viviparous female on *Polygonum*, 2) apterous viviparous female on Almond, 3) oviparous female; 4-8. ANTENNA 4) oviparous female, 5) male, 6) gynoparae, 7) apterous viviparous female on *Polygonum*, 8) apterous viviparous female on Almond; 9) CAUDA OF MALE; 10-11. CORNICLE 10) male, 11) apterous viviparous female on *Polygonum*.



winter on *Polygonum* do not exist. This leads to the co-presence of sexual and parthenogenetic cycles during that season.

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#### NOTE ON SOME EMESINAE (REDUVIIDAE, HEMIPTERA) FROM ISRAEL

*Ploiaria wahrmani* sp. n.

Apterous. Length of male 6.5, of female 7.0 mm; maximum width of abdomen of male 1.2, of female 2.0 mm.

General body colour, yellowish brown; an-

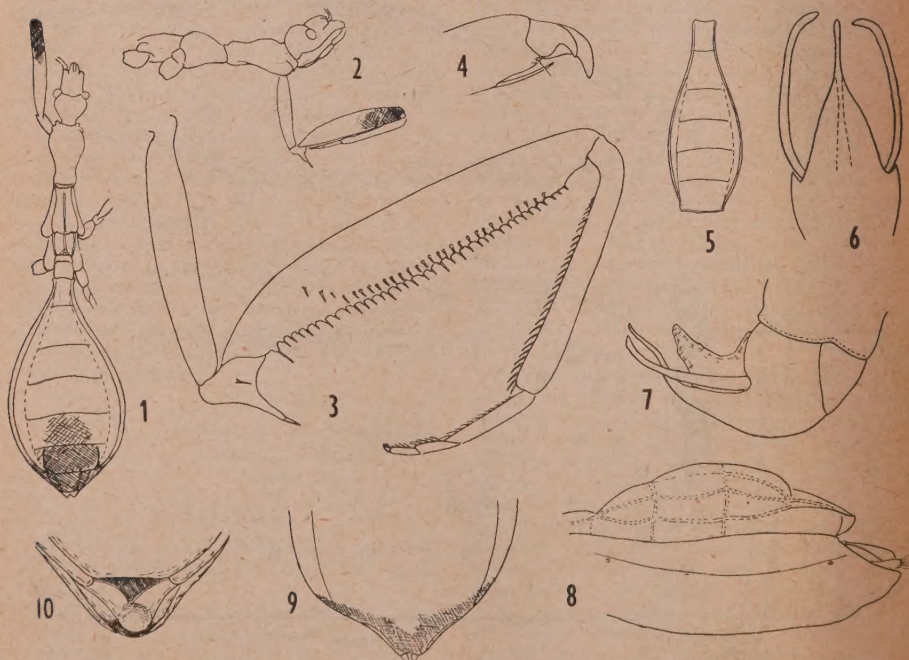
terior two fifths of fore femur, mid and hind femur subapically, the last two tergites of both sexes, as well as genitalia and apex of abdomen ventrally, dark piceous. Apex of mid and hind femora and bases of mid and hind tibiae, yellowish piceous. Body surface shining, abdomen slightly granulated.

Head as in figs. 1 and 2; ventral surface uniformly convex, anteocular and postocular region convex dorsally, without tubercles, ridges or processes. Eyes very small in both sexes. Rostrum as in fig. 2, second joint slightly shorter than first. Antennae very slender, with very short and inconspicuous pilosity only, in both sexes; length of first joint 3.5 mm; relative length of joints = 1:0.8:0.25:0.25.

Thorax as in figs. 1 and 2. Pronotum much longer than wide, swollen anteriorly, somewhat constricted before hind border. Mesonotum shorter than pronotum, slightly carinate longitudinally along median line; metanotum still shorter, distinctly carinate along middle.

Fore leg as in fig. 3; coxa about as long as head. Fore trochanter with a very long and stout ventral spiniferous process. Postero-

#### PLATE I



*Ploiaria wahrmani* sp.n.—Fig. 1, Female, general aspect; fig. 2, the same, lateral aspect of anterior portion of body; fig. 3, inner surface of fore leg; fig. 4, praetarsus and claws, high magnification; hypopygium and claspers, seen from behind; fig. 5, genital segments, lateral view; fig. 6, genital segments, lateral view; fig. 7, genital segments, lateral view; fig. 8, abdomen of female, lateral aspect; fig. 9, last tergites of female; fig. 10, genital segments of female, seen from behind.—Wygodzinsky del.

ventral series of fore femur composed of 35-40 short spiniferous processes, the spines short and stout, however much longer than their bases. Antero-ventral series composed of about 35 stout spinulets. Fore tibia slightly longer than half the length of the femur, ventrally with a series of stout spinelike bristles. Tarsus slightly longer than half the length of the tibia, its basal segment somewhat longer than the two apical segments together, ventrally with a series of spiniform bristles. Two unequal simple claws present (fig. 4). Mid and hind legs slender, without special characters, hind femora surpassing considerably apex of abdomen, their length 5 mm, length of hind tibiae 7.8 mm.

Abdomen of male (fig. 5) very slender at base, considerably widened towards middle, truncate apically. Tergites well delimited, sternites difficult to make out. Hypopygium large, its posterior process very elongate, upwardly directed; seen from behind, its base broad, subtriangular, its apical two fifths spinelike. Claspers very elongate, apically bent but not widened, attaining tip of hypopygial process (figs. 6-7).

Abdomen of female (fig. 1) wider than that of male, widest about middle. Genital segments as in figs. 8-10; last sternite slightly excavate at tip.

Material examined: Jerusalem, 1-IV-1948,

10-V-1948, 3-VI-1948, A. Moscona col. (1 ♂ holotype, 1 ♀ allotype, 1 ♀ paratype); Jerusalem, 15-XII-1949, J. Wahrman col. (1 ♀ paratype).

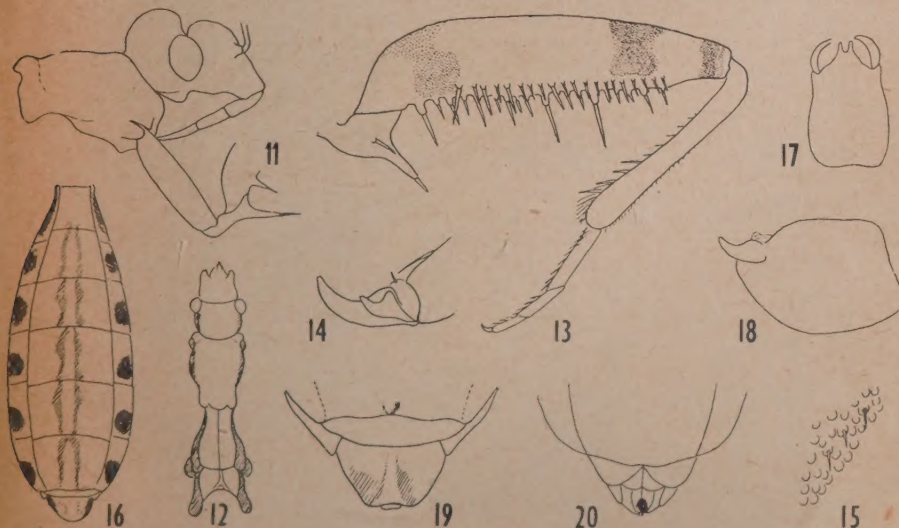
This species approaches the common widely distributed *Ploiaria domestica* Scopoli, 1786, from which it differs, among other characters, by its somewhat smaller size, different pattern, and the genital characters of the male, which are of the same general type, but differ in the shape of the posterior process of the hypopygium and the longer and more delicate claspers.

*Ploiaria mosconai* sp. n.

Apterous. Length of male 3.8, of female 4.3 mm; maximum width of abdomen of male 0.8, of female 0.95 mm.

General body colour stramineous. Piceous: a longitudinal streak on head laterally, from base of antennae through eyes to posterior lobe; ventral surface of first and the entire second segment of rostrum; antennae; fore coxa; a basal and a subapical spot as well as an apical annulum of fore femur; fore tibiae apically; mid and hind femora with exception of an apical whitish annulus; a large spot situated on the posterior half of all connexival segments, dorsally and ventrally; 1+1 somewhat interrupted submedian fasciae on

PLATE II



*Ploiaria mosconai* sp. n.—Fig. 11, head of male, lateral aspect; fig. 12, head and thorax, dorsal view; fig. 13, inner surface of fore leg; fig. 14, praetarsus and claws, high magnification; fig. 15, granulation of body surface, high magnification; fig. 16, abdomen of male, seen from above; fig. 17, hypopygium of male, seen from behind; fig. 18, hypopygium, lateral aspect; fig. 19, genital region of female, seen from behind; fig. 20, apex of abdomen of female, seen from below.—Wygodzinsky del.



dorsal surface of abdomen; lateral region of the female genital region, and the eighth and ninth sternite of the male, with the basal half of the claspers. Body surface subshining, somewhat granulated.

Head short and stout (figs. 11 and 12); ventral surface posteriorly with a large median tubercle; ante- and postocular region convex above. Eyes very small in both sexes. Rostrum as in fig. 11, second segment very slightly shorter than first, third about as long as first. Antennae very delicate, those of male with very long hairs in moderate number, on segments I and II. Length of first joint (in male) 2.1 mm; relative length of joints = 1:0.8:0.1:0.25.

Thorax as in figs. 11 and 12. Prothorax very short and stout, dorsally strongly widened on anterior half, constricted behind, hind border bisinuate. Mesonotum about as long as pronotum, slightly carinate along middle. Metanotum very short, carinate along centre.

Fore legs as in fig. 13; coxa about as long as head. Fore trochanter with a very long and stout ventral spiniferous process, its spine shorter than base. Anterior femur strongly widened subbasally. Posteroventral series of fore femur composed of 15-19 short and about 6 longer spines, the longest situated beyond middle. Antero-ventral series not interrupted at base, composed of about 7 larger and 12 smaller spines. Fore tibia slightly longer than half the length of femur, ventrally towards apex with elongate bristles, some of which are spine-like. Fore tarsus longer than half the length of tibia, its basal joint longest, the two apical ones subequal, together slightly longer than basal joint. Two claws, one of which very small. Mid and hind legs slender, without special characters, the hind femora surpassing slightly apex of abdomen; length of hind femur 3.0, of hind tibia 4.0 mm.

Abdomen of male (fig. 16) suboval, rather

elongate, hind border of last tergite rounded. Tergites and connexival segments very distinct, sternites difficult to make out; posterior border with a short bispinous process. Claspers short, curved, strongly widened at base (figs. 17-18).

Abdomen of female slightly wider than that of male; elevations at centre of hind border of tergites more distinct. Genital segments as in figs. 19 and 20.

Material examined: Jerusalem, 1-XII-1948, A. Moscona col. (2 ♂ ♂ paratypes); Jerusalem, 10-V-1948, A. Moscona col. 1 ♀ allotype; Jerusalem, 9-I-1949, A. Moscona col. (1 ♂ holotype).

The first two specimens are almost uniformly stramineous, the pattern being very difficult to make out. Owing to the complete identity of all morphological details, we do not hesitate to consider them as conspecific with the holotype and allotype. Identical considerable variability in the body colour has been observed in other species of the genus, p. ex. *Ploiaria dohrni* (Signoret, 1863).

This species comes very near to *Ploiaria gutturalis* Noulhier, 1895, as redescribed by Villiers (1943). *P. mosconai* differs from *P. gutturalis* by its somewhat smaller size, by the longer spines of the fore femur. The bisinuate hind border of the pronotum also seems to be a good differential character.

This note is part of a report on a small collection of REDUVIIDAE, which included 11 species of the subfamilies EMESINAE (*Ploiaria domestica* Scopoli, 1786), REDUVIINAE, STENOPODINAE and HARPACTORINAE, submitted for identification by the Department of Zoology of the Hebrew University.

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